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Ready Species One: Exploring the Use of Augmented Reality to Enhance Systematic Biology with a Revision of Fijian *Strumigenys* (Hymenoptera: Formicidae)

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Abstract

Advances in technology are rapidly changing the way people transmit, view, and interact with information. These advances offer new opportunities for researchers to share scientific discoveries with each other and the general public as never before. The field of revisionary biology has audiences confined to small groups of specialists, but the core task of systematic biology—documenting the endless forms of nature—is particularly well suited to capitalize on innovations in the realm of virtual, mixed and augmented reality. Interactive three-dimensional (3D) digital models of biological specimens can help bridge barriers across scientific disciplines by circumventing technical jargon, and also promise to open exciting new vistas for public engagement. Here, we explore the potential of augmented reality for communicating the discovery of new species. As a test case, we revise a radiation of *Strumigenys* Smith (Hymenoptera: Formicidae) miniature trap-jaw ants in Fiji. In addition to traditional revisionary elements, we present the augmented reality application 'Insects3D' built specifically for this study. The application runs on mobile devices and allows users to interact with X-ray microtomography-derived 3D specimen models and visualize 3D geographic distribution maps. We recognize 23 species in Fiji, including 6 new species: *S. anorak* n. sp., *S. artemis* n. sp., *S. avatar* n. sp., *S. gunter* n. sp., *S. oasis* n. sp., and *S. parzival* n. sp. This study demonstrates the potential of leveraging 3D data and technology for a more interactive systematic biology, and the need for research programs to develop robust and generalized tools to realize this potential.

Key words: augmented reality, specimens, biodiversity, microtomography, taxonomy

For a bunch of hairless apes, we've actually managed to invent some pretty incredible things. — Ernest Cline, Ready Player One

Taxonomy—the science of classifying life on earth—is foundational to organismal biology. As elder statesmen of biodiversity science have noted, 'The goal of discovering, describing, and classifying the species of our planet assuredly qualifies as big science' (Wheeler *et al.* 2004). During the turn of the 21st century, the scientific community began discussing both the biodiversity crisis and the taxonomic impediment: the pace of species extinction was accelerating even as taxonomic research was losing prestige, resources, and talent (Pimm *et al.* 1995, Godfray 2002, Godfray and Knapp 2004, Wheeler 2004). Were taxonomists to thrive in the molecular era, taxonomy would need to adapt.

Two crucial developments of taxonomy in the 21st century are the integration of molecular evidence and the adoption of new specimen imaging technologies. The marriage of molecular data to traditional morphology has made taxonomy a more robust science. Genetic analysis has proved indispensable for stabilizing higher level classification, rooting out morphological homoplasy, and providing early scaffolds for large taxonomic revisions (Padial *et al.* 2010, Schlick-Steiner *et al.* 2010).

Although taxonomy benefits from the integration of molecular data, the discipline remains rooted in descriptive and analytical morphology. In this respect, the integration of new imaging technologies has arguably had more impact on the scientific quality and clarity of new species descriptions than has the inclusion of genetic data. Modern imaging is especially crucial for studying small invertebrates, which compose the majority of both described and undescribed species. As example, the broad adoption of focus stacking technology during the past two decades has revolutionized photography of arthropod specimens by eliminating depth of field constraints (Blagoderov *et al.* 2012, Brecko *et al.* 2014). In addition

to enhancing the quality of new species descriptions, online image repositories of type specimens enable faster species descriptions by reducing time-intensive museum visits and specimen loans.

The most compelling advances in biological specimen imaging are arguably coalescing around three-dimensional (3D) imaging and processing technologies capable of generating virtual specimen models. The two most prevalent 3D imaging technologies used by organismal biologists—and invertebrate zoologists in particular— are micro-computed tomography (micro-CT) (Faulwetter *et al.* 2013, Akkari *et al.* 2015, Hita Garcia *et al.* 2017b, Ijiri *et al.* 2018) and photogrammetry (Nguyen *et al.* 2014, Gutiérrez-Heredia 2015, Qian *et al.* 2015, Galantucci *et al.* 2016, Gutierrez-Heredia *et al.* 2016, Sosa *et al.* 2016). Although 3D imaging of biodiversity collections is in its infancy, access to micro-CT scanners in biology departments and natural history institutions is increasing. Simultaneously, more cost-effective photogrammetry systems are being developed. Consequently, biologists are publishing large datasets of 3D specimen models on websites such as Sketchfab (Sketchfab 2018), Zoosphere (Zoosphere 2018), and Morphosource (Morphosource 2018, Watkins-Colwell *et al.* 2018).

The expanding availability of 3D specimen data is coinciding with a bourgeoning array of tools for 3D model visualization. Augmented reality (AR), for example, is an emerging technology capable of superimposing 3D computer-generated images on a user's view of the real world. As testament to the technology's growth, the global augmented reality market was valued at USD 3.33 billion in 2015 and is expected to reach approximately between USD 80 and 130 billion in 2021 (Zion Market Research 2017). Whereas users view *only* computer-generated images in virtual reality (VR), the view in AR is a composite of the real world and virtual world. Our focus on AR, rather than VR, acknowledges that while access to the head-mounted displays (HMDs) required for experiencing VR is currently limited, nearly everyone carries an AR compatible mobile device, such as a smartphone or tablet.

Biological applications of augmented reality have primarily been the provenance of the medical field (Azuma 1997). Comparatively little attention has been given to the implications of AR for biodiversity research and outreach (Bimber *et al.* 2002, White *et al.* 2006, Yeh *et al.* 2006, Barry *et al.* 2012, Chiang *et al.* 2014, Seltmann *et al.* 2017). Moreover, the application of AR to taxonomic research has thus far received mention in passing only (Sosa *et al.* 2016). The lack of connectivity between taxonomic research and AR is somewhat surprising, as museums are both integral to taxonomic research and among the earliest institutional adopters of AR technology (Wojciechowski *et al.* 2004, Debenham *et al.* 2011, Yoon *et al.* 2012). On the basis of our literature review, we are unaware of any published taxonomic studies that explicitly include visual markers for displaying specimen models in augmented reality.

In previous contributions (Fischer *et al.* 2016; Sarnat *et al.* 2016, 2017; Agavekar *et al.* 2017; Hita Garcia *et al.* 2017b, 2017a; Staab *et al.* 2018), we focused on the use of 3D X-ray imaging for systematics. The aforementioned studies included passive media (e.g., 3D models flattened into 2D figures, video of rotating 3D models) and interactive media (e.g., rotatable 3D models embedded in interactive PDFs). Here we explore how 3D imaging technology can create *immersive* media for use in organismal biology.

Statement of Purpose

In this paper, we present proof-of-concept examples for how augmented reality can add research value to systematic biology.

Specifically, we demonstrate how mesh models generated from the morphological and geographic data of newly described *Strumigenys* Smith, 1860 (Hymenoptera: Formicidae) ants can be viewed and manipulated in three dimensions using commonplace mobile devices. We present methods and results for all stages of AR deployment, including specimen scanning, mesh model creation, marker development, and mobile app development. We conclude our discussion by critiquing opportunities and challenges for using AR technologies to enhance biodiversity research, education, and outreach. The study provides direction for future integration of emerging technologies such as augmented reality and virtual reality into specimen-based research.

Strumigenys

The taxonomic focus of the study presented here are *Strumigenys* ants from the Fiji Islands. *Strumigenys*—known also as miniature trap-jaw ants—are diminutive predators that specialize in capturing minute arthropods. These huntresses most often nest and forage in leaf litter, topsoil and decaying wood and form small and usually monogynous colonies (Bolton 1999). The most prevalent prey are entomobryomorph Collembola, but they will take other small arthropods as well (Wilson 1954, Brown 1971, Masuko 1985, Dejean 1987). *Strumigenys* species are primarily distributed across tropical and subtropical rainforests and are most commonly collected using leaf litter extraction methods such as Berlese funnels or Winkler traps.

Strumigenys ants are striking in appearance. They exhibit elongated, pyriform heads flattened along the dorsoventral axis. They produce a rich variety of highly modified hairs from thick, flattened, and spatulate to gossamer thin, thread-like, and twisting. Nearly all produce mysterious sponge-like outgrowths referred to as spongiform appendages that emanate from the waist. The mandibles of many are shaped into outlandishly long levers spiked at the tip with long piercing teeth.

Long-mandible *Strumigenys* are commonly referred to as trap-jaw ants on account of their mandibles' spring-loading mechanism which is triggered to snap shut by the touch of suitable prey. Though trap-jaw mechanisms evolved in at least three ant subfamilies and nine genera, the vast majority of trap-jaw ants belong to the genus *Strumigenys* (Larabee and Suarez 2014). Not all of the 800+ described *Strumigenys* species (Bolton 2018) are trap-jaw ants. Many species previously placed in distinct genera on account of their variant jaw shape or number of antennal segments (Bolton 2000) are now placed in *Strumigenys* based on molecular evidence of shared ancestry (Ward *et al.* 2015). The taxonomic history of *Strumigenys* has been extensive and occasionally contentious (Baroni Urbani and de Andrade 2006, Bolton 2006). A comprehensive list of taxonomic studies treating *Strumigenys* is included in Bolton (2000) and Baroni Urbani and de Andrade (2007).

The tropical islands of the Fijian archipelago host an exceptionally rich fauna of *Strumigenys*. In total, 23 species are now known from the archipelago, including 6 that are described here for the first time. Two species (*S. membranifera* Emery and *S. rogeri* Emery) are introduced from Africa and an additional tramp species (*S. godeffroyi* Emery) is most likely native to Southeast Asia. The remaining 20 species are considered endemic to Fiji, although 1 species (*S. mailei* Wilson & Taylor) is also recorded from Samoa.

The first treatment of Fiji's *Strumigenys* species was presented by Mann (1921) in his monograph on the archipelago's ants. In addition to listing *S. godeffroyi*, Mann described five species—*S. jepsoni*, *S. nidifex*, *S. scelestus*, *S. vitiensis*, *S. wheeleri*—although the latter

two were later synonymized with *S. membranifera* and *S. tumida* Bolton, respectively. A key to these six species was included and the genus was briefly discussed with respect to the high number of species on the archipelago. Wilson and Taylor (1967) described *S. mailei* from Samoa, and designated as paratype a worker collected from the uplands of Viti Levu by E.C. Zimmerman in 1938. Dlussky (1993) described *S. chernovi* from Fiji in a study of the southwestern Pacific *Strumigenys*. Bolton (2000) described eight new species of Fijian *Strumigenys* in his global revision of *Strumigenys* (*S. basiliska, S. daithma, S. ekasura, S. frivola, S. panaulax, S. praefecta, S. sulcata, S. trauma* (= *Pyramica trauma*) and provided *S. wheeleri* Mann with the replacement name *S. tumida*.

Sarnat and Economo (2012) presented a diagnostic key, species accounts, specimen photographs, and distribution maps for all the valid *Strumigenys* known from Fiji along with seven putatively undescribed species. After further review of these seven morphospecies discussed in Sarnat and Economo (2012) we propose here that five represent new species (*S. anorak* **n. sp.**, *S. artemis* **n. sp.**, *S. avatar* **n. sp.**, *S. gunter* **n. sp.**, and *S. oasis* **n. sp.**). Comparison with additional type material also suggests that the specimens treated in Sarnat and Economo (2012) as *S. panaulax* Bolton constitute a distinct species, described here as *S. parzival* **n. sp.**

The present work is an ongoing effort (Sarnat 2006; Lucky and Sarnat 2008; Sarnat 2008; Sarnat and Economo 2012, 2013; Hita Garcia *et al.* 2015; Fischer *et al.* 2016) to describe Fiji's rich and highly endemic ant fauna. Taxonomy is the foundation of organismal biology, and these morphological studies have prompted new hypotheses concerning taxon cycles (Economo and Sarnat 2012, Matos-Maraví *et al.* 2018a), island biogeography (Lucky and Sarnat 2010, Sarnat and Moreau 2011, Clouse *et al.* 2015, Economo *et al.* 2017, Matos-Maraví *et al.* 2018b), and functional ecology (Sarnat *et al.* 2017).

The Fijian *Strumigenys* are a model group for studying rapid morphological and ecological radiation of social insects on island systems. Analysis of molecular data from a global sampling of *Strumigenys* suggests the long-mandible Fijian endemics are all descended from a single colonist ancestor (Liu et al. unpublished data). The in situ evolution of such dramatic morphological disparity strongly contradicts previous biogeographic hypotheses based on morphological observation. Bolton assigned each of Fiji's native and endemic *Strumigenys* to species groups (Table 1). Given that none of the listed groups or complexes are composed strictly of Fijian species, Bolton's assignments assume Fijian endemic *Strumigenys* are descended from no fewer than six independent colonization events.

Although the meticulous global revision was explicit that many of the Fijian species did not neatly conform to their assigned groups— and that the assignments more accurately reflected morphological similarity than phylogenetic proximity—the extent of evolutionary convergence with distantly related Indoaustralian congeners was not anticipated by Bolton (2000) or Sarnat and Economo (2012). That all long-mandible Fijian endemic *Strumigenys* are monophyletic is remarkable not only because the morphology of *S. nidifex* Mann so closely parallels that of the distantly related *szalayi*-group, or because the morphology of *S. basiliska* Bolton so closely parallels that of the distantly related *biroi*-group, but because these two disparate species together with their endemic congeners—even the aberrant *S. oasis*—all descended from a single common ancestor in the putatively recent past (Lucky and Sarnat 2010, Sarnat and Moreau 2011, Sarnat and Economo 2012).

Methods

Species identification and delineation

Strumigenys is relatively unique among ant genera with respect to its abundance of morphological characters—particularly hairs, spongiform tissues, mandibles, and sculpture. Despite their minute size and rich taxonomic diversity, species of *Strumigenys* are thus readily discerned from one another even when few specimens are available for analysis. Initial specimen identification morphospecies designation was conducted as part of Sarnat and Economo (2012).

Table 1. Fijian *Strumigenys* arranged by species name. Species group names and group-complex names to which Bolton (2000) assigned Fijian *Strumigenys* are listed. Species assigned by Bolton (2000) to *Pyramica* are also noted

Species	Status	Bolton group/genus	Group complex
S. anorak, **n. sp.**	endemic	—	—
S. artemis, **n. sp.**	endemic	—	—
S. avatar, **n. sp.**	endemic	—	—
S. basiliska Bolton	endemic	*biroi*	—
S. chernovi Dlussky	endemic	*godeffroyi*	*smythiesii*
S. daithma Bolton	endemic	*caniophanes*	—
S. ekasura Bolton	endemic	*godeffroyi*	*smythiesii*
S. frivola Bolton	endemic	*rofocala*	—
S. godeffroyi Mayr	introduced	*godeffroyi*	—
S. gunter, **n. sp.**	endemic	—	—
S. jepsoni Mann	endemic	*godeffroyi*	*smythiesii*
S. mailei Wilson & Taylor	native	*godeffroyi*	*signeae*
S. membranifera Emery	introduced	(*Pyramica*) *membranifera*	—
S. nidifex Mann	endemic	*szalayi*	—
S. oasis, **n. sp.**	endemic	—	—
S. panaulax Bolton	endemic	*godeffroyi*	*smythiesii*
S. parzival, **n. sp.**	endemic	—	—
S. praefecta Bolton	endemic	*godeffroyi*	*signeae*
S. rogeri Emery	introduced	—	—
S. scelesta Mann	endemic	*godeffroyi*	*smythiesii*
S. sulcata Bolton	endemic	*godeffroyi*	*signeae*
S. trauma (Bolton)	endemic	(*Pyramica*) *capitata*	—
S. tumida Bolton	endemic	*godeffroyi*	*signeae*

Bolton's (2000) authoritative global revision of *Strumigenys* was used as the primary identification reference together with examination of type material for all available Fijian endemic *Strumigenys*. Specimens which could not be identified using the aforementioned references were compared with invasive and tramp *Strumigenys* before publishing them as morphospecies in Sarnat and Economo (2012). The species concepts presented here are also supported by rigorous phylogenetic analysis of genome-wide SNP markers (Liu et al. in review) that includes 18 of the putative 23.

X-ray microtomography

Micro-CT scanning

We captured X-ray microtomographic scans of 15 *Strumigenys* specimens representing all species endemic to Fiji for which suitable material was available. The specimens were left attached to their paper point, which was clamped to a holding stage. Scan settings were selected according to yield optimum scan quality and primarily follow Hita Garcia *et al.* (2017a) and Hita Garcia *et al.* (2017b). In contrast to the former study, we performed only full body scans and refrained from including standardized scans of head, mesosoma, and metasoma. All micro-CT scans were performed using a Zeiss Xradia 510 Versa 3D X-ray microscope operated with the Zeiss Scout-and-Scan Control System software (version 11.1.6411.17883). Specimen data and scanning parameters are provided in Table 2.

Virtual reconstruction and postprocessing of raw data

Three-dimensional reconstructions of the resulting scan projection data were generated using the Zeiss Scout-and-Scan Control System Reconstructor (version 11.1.6411.17883) and saved in DICOM file format. Post-processing of DICOM raw data was performed with Amira software (version 6.2). Virtual examinations of 3D surface models were performed by using either the 'volren' or 'volume rendering' functions. Desired volume renderings were generated by adjusting color space range to a minimum to ensure the exterior surface of specimens remained visible at the highest available quality. Three-dimensional models were rotated and manipulated to allow a complete virtual examination of the scanned specimens. Images of shaded surface display volume renderings were made with the 'snapshot' function at the maximum resolution (approximately 1900 by 893 pixels).

Three-dimensional model development and optimization for augmented reality applications

Computer generated 3D specimen models

The 3D mesh models presented here were generated using micro-CT volumetric data. Each model is composed of large sets of connected vertices and faces (polygons) that can be rendered or streamed in real time. The tradeoff between detail and performance is inherent to 3D modeling (Franco *et al.* 2004). Increasing model detail decreases model performance: detail is measured by the number of polygons (or vertices) in the model, performance is measured by the processing time needed to render the model

Micro-CT is an effective method for capturing internal structures and reconstructing surface volumes. However, CT volumes do not capture surface appearance such as colors and textures. To create specimen models with both morphologically accurate surface volumes and visually accurate colors and textures, we mapped 2D specimen photographs onto the CT surface volume using the application Zbrush.

We developed two versions of 3D specimen models for each of the newly described *Strumigenys* species: maximum detail and optimized.

Table 2. Micro-CT scanning parameters arranged by species name

Taxon code	Specimen code	Caste	Date	Voxel size	Exposure time (s)	Source distance (mm)	Detector distance (mm)	Power (W)	Voltage (kV)	Amperage (µA)
S. anorak	CASENT0186900	worker	17 Dec. 2017	3.8979	0.5	−15	11	5	60	84
S. artemis	CASENT0186982	worker	16 Dec. 2017	1.8136	1.0	−11	30	5	60	84
S. avatar	CASENT0185902	worker	17 Dec. 2017	4.6916	1.0	−2.5	11	5	60	84
S. basiliska	CASENT0185655	worker	1 July 2018	2.4775	0.5	11	19	6	70	86
S. chernovi	CASENT0184909	worker	1 July 2018	2.0646	0.6	11	25	6	70	85
S. ekasura	CASENT0184622	worker	1 July 2018	1.8129	1.0	11	30	5	70	72
S. frivola	CASENT0186834	worker	1 July 2018	2.2523	0.6	11	22	5	60	83
S. gunter	CASENT0184984	worker	16 Dec. 2017	2.065	1.0	−11	25	5	60	84
S. mailei	CASENT0184653	worker	1 July 2018	1.9559	0.7	11	27	6	70	86
S. nidifex	CASENT0185548	worker	30 June 2018	3.503	0.7	14	13	4	50	80
S. oasis	CASENT0185751	worker	16 Dec. 2017	2.065	1.0	−11	25	5	60	84
S. parzival	CASENT0186960	worker	17 Dec. 2017	2.0649	1.0	−11	25	5	60	84
S. praefecta	CASENT0186943	worker	1 July 2018	2.3851	1.2	12	22	4	50	79
S. salcata	CASENT0185705	worker	30 June 2018	3.5032	0.8	14	13	4	50	80
S. tumida	CASENT0185699	worker	30 June 2018	3.2434	0.8	12	13	4	50	80

The maximum detail models were generated to preserve as much of the original specimen surface topology as data allowed. All polygons are preserved from the original micro-CT scans described in the preceding section. The target audiences of the maximum detail models are colleagues interested in using the models for scientific research.

The optimized models were generated to preserve the maximum level of detail that can be smoothly rendered by an iPhone 6s or equivalent mobile device. In order to determine a suitable tradeoff of detail versus performance, we created four additional models of varying polygon numbers (1m, 500k, 100k, 14k) derived from the maximum quality model (8.1m polygons) of the *Strumigenys avatar* holotype (CASENT0185902). Of the optimization trials, the 500k polygon model was the highest-detail model that reliably rendered using the augmented reality function in the Sketchfab app with an iPhone 6s (the 1m and 8.1m polygon models proved too large for rendering). Based on the optimization trial results for *S. avatar*, we optimized the models of the additional five new species to 500k polygons.

The first step of the optimization process was to use the Zbrush digital sculpting application to remove as many noninformative polygons from the model as possible, specifically polygons representing the paper point and glue used for mounting the ant specimen. The number of polygons was reduced using the DynaMesh tool within the Zbrush application. Rather than distribute polygons equally across the entire mesh model, priority was given to parts of the specimen that are morphologically complex, such as the head. The mesh was prepared for texture mapping using the ZRemesher tool of Zbrush which projects a 2D image to a 3D model surface. The model was then imported into the application 3Ds Max and unwrapped (separated and unfolded) for projecting the texture. The images used for texture were the three standard 2D photographs of each respective specimen. The Zbrush application was used for painting and applying the 2D photographs onto the 3D model. The final step in the process was to export the model to FBX and to upload together with the MTL file and texture files to Sketchfab.

Map model

The goal of three-dimensional modeling of geographic terrain is to displace a textured 3D planar mesh vertically using the heightmap, smooth the mesh, simplify the mesh, and export the mesh as a 3D model. Landsat 8 imagery of the Fiji Islands pansharpened to 15 meters was used to create a natural color texture overlay for a 3D elevation model. Multiple Landsat 8 images were color matched and mosaicked in ENVI 5.1 and retouched and further color matched in Adobe Photoshop to create a seamless cloud-free landscape. Date ranges for the imagery used are from 22 January 2014 to 20 March 2018 and were chosen from among 1,440 different images of mixed seasons. 3D map elevation data were derived from the Shuttle Radar Topography Mission (SRTM) 1 arc-sec global dataset. Voids present in the SRTM dataset were filled with the void-filled SRTM 3-arc-sec product. Aberrations and spikes in the SRTM data were smoothed using the 'Spot Healing Brush' in Adobe Photoshop. The 3D elevation model was made using Blender 2.79b (www.blender.org). The modified SRTM elevation raster, Landsat 8 imagery, and species locations were imported to Blender using the BlenderGIS plugin (https://github.com/domlysz/BlenderGIS). The SRTM elevation raster was converted to a mesh using the 'Displace' modifier in Blender with a strength of zero applied to a mesh of 19.2 million vertices. The final mesh was decimated and smoothed to simplify the geometry and then combined with a normal map generated from the high-density mesh to recover detail and remain performant. Ocean waves were generated using Blender's 'Ocean' modifier on a separate surface and merged with the normal map for elevation dataw.

Finally, the models were added onto the Sketchfab (Sketchfab, New York City, New York), a 3D content publishing platform to provide a website interface for interactive manipulation of the model and future presentation and annotation. Sketchfab is a platform to share and discover 3D, virtual reality, and augmented reality content. All models are available for viewing and manipulating at the following URL [https://sketchfab.com/arilab/collections/strumigenys-species-from-fiji].

Augmented reality app development

We designed the mobile app 'Insects3D' for interacting with three-dimensional models of taxonomic content in augmented reality. The experience was developed in Unity 2018.2.13f1 using the Vuforia 7.2.23 Unity package, which enabled AR in the application. Extended tracking, which enabled ground detection system and improved tracking stability, was implemented using Apple ARKit. The experience was designed for Apple iPhones and Apple iPads with AR-capable processing power (6S and above for iPhone).

Data availability

All specimens used in this study have been databased and the data are freely accessible on AntWeb (http://www.antweb.org). Each specimen can be traced by a unique specimen identifier attached to its pin. The cybertype/virtual datasets provided in this study consist of the full micro-CT original volumetric datasets (in DICOM format). All data have been archived and are freely available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.1f9d55b). In addition to the cybertype data at Dryad, we also provide freely accessible 3D surface models of all treated species on Sketchfab in the '*Strumigenys* species from Fiji' collection <https://skfb.ly/6FnYo>.

Material examined and type depositories

Museum abbreviations

ANIC	Australian National Insect Collection (Canberra, Australia)
BPBM	Bernice Pauahi Bishop Museum (Honolulu, HI, USA)
MCZC	Museum of Comparative Zoology, Harvard, Cambridge (Boston, MA, USA)
OIST	Okinawa Institute of Science and Technology (Okinawa, Japan)
USNM	United States National Museum of Natural History (Washington D.C., USA)

Study specimens

The material examined in this study was collected from 2002 to 2007, and includes specimens collected as part of the Fiji Terrestrial Arthropod Survey (Evenhuis and Bickel 2005) and other collections made by the authors (Sarnat and Economo 2012). The ant specimens were collected and stored in ethanol before they were dry mounted on paper tips and insect pins and are currently deposited in the ant collection in OIST, Okinawa, Japan. The holotype material designated here will be deposited in the BPBM. Paratypes will also be deposited in MCZC and USNM. Readers are referred to the relevant species accounts in Sarnat and Economo (2012) for a comprehensive list of all material examined. All specimens and their associated data can be accessed by using the advanced search option in Antweb.org. Additional images along with additional specimen, collection and locality data for all species treated here are available on Antweb.org.

Standard measurements and indices

Measurements and terminology follow Bolton (2000). All measurements are expressed in millimeters. Measurements presented for all previously described species, with the exception of *S. trauma*, are taken from Bolton (2000). Measurements presented for *S. trauma* include original data taken from Fijian specimens.

MsL   *Mesosoma length* (= Weber's Length, = Alitrunk length). The diagonal length of the mesosoma in profile from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.

CI   *Cephalic index*. HW/HL × 100.

EL   *Eye length*. Maximum diameter of the eye measured in lateral view.

FI   *Femur index*. FL/HW × 100.

FL   *Metafemur length*. Maximum length of hind femur measured from junction with trochanter to junction with tibia.

HL   *Head length*. The length of the head capsule excluding the mandibles, measured in full-face view in a straight line from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin. In species where one or both of these margins is concave the measurement is taken from the mid-point of a transverse line that spans the apices of the projecting portions.

HW   *Head width*. The maximum width of the head in full-face view, excluding the eyes.

MI   *Mandibular index*. MdL/HL × 100.

MdL   *Mandible length*. The straight-line length of the mandible at full closure, measured in the same plane for which the HL measurement is taken (i.e., full-face view), from the mandibular apex to the anterior clypeal margin, or to the transverse line connecting the anteriormost points in those taxa where the margin is concave medially.

PI   *Pronotal index*. PW/HW × 100.

PW   *Pronotal width*. The maximum width of the pronotum in dorsal view.

SI   *Scape index*. SL/HW × 100.

SL   *Scape length*. The maximum straight-line length of the scape, excluding the basal constriction or neck that occurs just distal of the condylar bulb. (In taxa with a hypertrophied subbasal lobe on the scape SL is measured from the tip of the subbasal lobe to the scape apex.)

TL   *Total length*. The total outstretched length of the ant from the mandibular apex to the gastral apex; when measured in profile the sum of MdL + HL + MsL + lengths of waist segments + length of gaster.

Nomenclature

This paper and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:F19C2E83-6D10-4EA8-BD17-A9C5C5ED73C3

Results and Discussion

Three-dimensional model development and optimization for augmented reality applications

Insects3D: an augmented reality app for visualizing specimen models

Insects3D is an iOS compatible app designed as a proof-of-concept solution for integrating augmented reality content with systematic biology. Insects3D is available as a free download from the Apple App Store <https://apps.apple.com/us/app/insects3d/id1451203549>. A short video demonstrating the features and functionality of Insects3D is available from the online version of this article (Supp. Vid. S2) and on YouTube <https://youtu.be/uSy1M7zPjIY>.

The Insects3D app allows users to visualize 3D specimen models of the six new *Strumigenys* species described here using two different modes (Fig. 1). In 3D mode, the models display on-screen and can be rotated along three axes using touch gestures. In AR mode, the models are anchored either to a visual marker or to a user-selected surface. The computer-generated models display on the device's camera screen and behave as if they were fixed objects in the room. The user observes the models from different angles either by keeping the mobile device stationary and moving the visual marker, or by keeping the marker stationary and moving the mobile device.

Users select which species to visualize using the taxon selector dropdown menu and toggle between specimen model and map model by tapping the specimen/map icon. The following features are available in both 3D and AR mode: a) pinch-to-resize [scales size of specimen and map model], b) spin [rotates specimen model 360° on vertical axis], c) texture slider [increases/decreases opacity of specimen model texture (e.g., surface color)].

The app recognizes two classes of markers: universal markers and species-specific markers. Visual markers are typically graphic symbols that can be recognized with machine vision and accessed using cameras in mobile devices (Zhou *et al*. 2008, Costanza and Huang 2009, Alakärppä *et al*. 2017). The universal marker (Supp. Fig. 1 [online only]) is a vector-based illustration of a *Strumigenys* head in face-view. Once scanned with the device camera in AR mode of the app, the universal marker allows users to select across all six specimen models. The species-specific markers are the plates of shaded surface display volume renderings presented for each of the six new species presented here. Scanning micro-CT plates labeled 'AR marker' with the Insects3D app in AR mode will trigger the display of the respective specimen model.

Texture mapping

After evaluating our texture mapping results, we suggest several modifications to improve future methods. With respect to texture mapping, our primary objective in this study was to determine whether adequate results could be achieved using only the three standard 2D specimen photographs (head, profile, dorsal). Although the addition of color to the mesh models presented here may make them more engaging for a nonscientific audience, they are not satisfactory for scientific research applications. Quality would most certainly increase to the extent photographs from additional angles are incorporated. Constraining our sources to the three standard images limited the texture quality of the models. Much of the surface detail preserved in the 500k polygon micro-CT model (e.g., individual ommatidia) was masked by low-resolution texture imagery. As result, comparable visual quality could be achieved by using lower polycount and faster performing mesh models.

Upon reviewing the nascent literature, we propose 360° image-based techniques, such as those used in photogrammetry, are more economical and will arguably yield higher quality texture results—as measured by verisimilitude and processing requirements—than those achieved by our use of only three standard images mapped onto CT-based mesh models. As caveat, CT-based techniques are superior to image-based techniques for capturing internal and occluded structures, and new methods for combining the two are being developed with results more impressive than those presented here (Ijiri *et al*. 2018).

Fig. 1. Screenshots illustrating available features in the Insects3D app. The Insects3D app is available for free on the Apple App Store and is compatible with iPhone and iPad devices. A video demonstrating the features and functionality of Insects3D is available from the online version of this article (Supp. Vid. S2) and on YouTube <https://youtu.be/uSy1M7zPjIY>. https://youtu.be/uSy1M7zPjIY. (A) 3D mode displaying specimen model of *Strumigenys avatar*. (B) 3D mode displaying map model of *S. avatar*. (C) Augmented reality (AR) mode projecting specimen model of *S. avatar* using Fig 13 as the marker. (D) AR mode projecting map model of *S. artemis* using the universal marker (Supp. Fig.1 [online only]). (E) 3D model of *S. avatar* projected onto the surface of a laboratory desk using the 'place anywhere' function

Opportunities and challenges for AR enhanced biodiversity science

With respect to the study presented here, the current state of AR technology suggests its value to biodiversity education outstrips its value to taxonomic research. The models that worked best on our mobile devices with respect to loading time and rendering speed were the ones with the lowest visual quality—and hence, most limited taxonomic value. And even if the highest visual quality models were loaded quickly and rendered smoothly, using a mobile device for model viewing is cumbersome and not necessarily conducive to a taxonomic description workflow that already includes microscopes, keyboards, and computer screens.

While AR added limited value to the taxonomic study presented here, it is worth discussing the potential of AR technology as it relates to specimen-based research. A future—albeit a distant one—is imagined in which a researcher surrounded by museum drawers accesses specimen data in AR using a mobile device. Consider, for example, a specimen AR app similar to the one presented here is installed on your phone. You pull the *Strumigenys avatar* holotype out from the drawer, place it in an empty unit tray or on a stage, and use your app to scan the printed 'CASENT0185902' unique specimen identifier label. Without needing computer or microscope, you examine from all angles a 3D virtual model using your phone screen. You view a 3D map of the collection locality to ascertain biogeographic factors. If the collection site was captured with 360° photo or video, you point your phone up to view the type locality's canopy cover, down for ground cover and substrate, straight ahead and all around for vegetation composition.

In contrast to AR, the micro-CT technology used to generate virtual specimen models added discernable value to our taxonomic workflows. For example, incorporating 3D models into our species description and diagnostic key workflows decreased the time and risk of handling type specimens. Unlike our phones, which were unable to smoothly render high polycount mesh models, our personal computers had no difficulty processing the highest quality scans. There were numerous occasions whereupon the character states such

as shape and sculpture were rendered clearly enough in the 3D specimen models as to be used for species description without needing to physically handle the type specimens. Likewise, viewing multiple models simultaneously was useful for designing the diagnostic key. We found the 3D models to be preferable to 2D photographs for examining shape and sculpture, but they were inadequate for examining pilosity—a result also discussed by Hita Garcia *et al.* (2017b).

Although we advocate for increasing the use of 3D technologies in taxonomic research, we caution that its inclusion—as with molecular data—should not be prerequisite for the publication of species descriptions. In our introduction, we argued that new imaging technologies have increased the rate and clarity of species descriptions. While we believe this claim true for focus-stacking technologies used for 2D specimen photography, it is less applicable to 3D imagining—at least when microtomographic methods are used. With respect to taxonomic research, 3D microtomography is arguably more similar to molecular data. Both add significant value to taxonomy but also significant investments in time, training, and treasure. Given the enormous numbers of undescribed species relative to the few numbers of taxonomists and slow publication rate, adding additional constraints is not necessarily a winning strategy for addressing the taxonomic impediment.

Whereas the value of AR technology to taxonomic research is disputable in its current state, AR has demonstrated broad value in educational contexts (Wu *et al.* 2013, Akçayır and Akçayır 2017, Chen et al. 2017)—and biodiversity education specifically (White *et al.* 2006, Yeh *et al.* 2006, Barry *et al.* 2012, Chiang *et al.* 2014, Seltmann *et al.* 2017). The technology already exists for taxonomists to upload 3D specimen models to online databases, and for end users to view models on their mobile devices using free iOS and Android apps such as Sketchfab, Augment, and similar platforms. Student posters at scientific conferences, curated exhibits at natural history museums, textbooks in classrooms could all use AR to make taxonomic subjects available to large audiences. Being able to interact with large-scale, 3D and potentially natural-color models using one's own phone or tablet is a more immersive experience than viewing a small, static, 2D photograph of the same specimen. In many ways, interacting with specimen models using AR technologies offers a compelling alternative to microscopes. Microscopes are expensive, limited in availability, and difficult to use without prior training. With AR, an experience similar to viewing minute invertebrates on a rotating stage under strong magnification can be achieved using the phone in one's pocket.

Taxonomic Analysis

Synoptic list of *Strumigenys* species known from Fiji

S. anorak, **n. sp.**
S. artemis, **n. sp.**
S. avatar, **n. sp.**
S. basiliska Bolton
S. chernovi Dlussky
S. daithma Bolton
S. ekasura Bolton
S. frivola Bolton
S. gunter, **n. sp.**
S. godeffroyi Mayr
    = *S. butteli* Forel
    = *S. geococci* Calilung
    = *S. indica* Forel
S. jepsoni Mann
S. mailei Wilson & Taylor
S. membranifera Emery
    = *S. foochowensis* Wheeler
    = *S. marioni* Wheeler
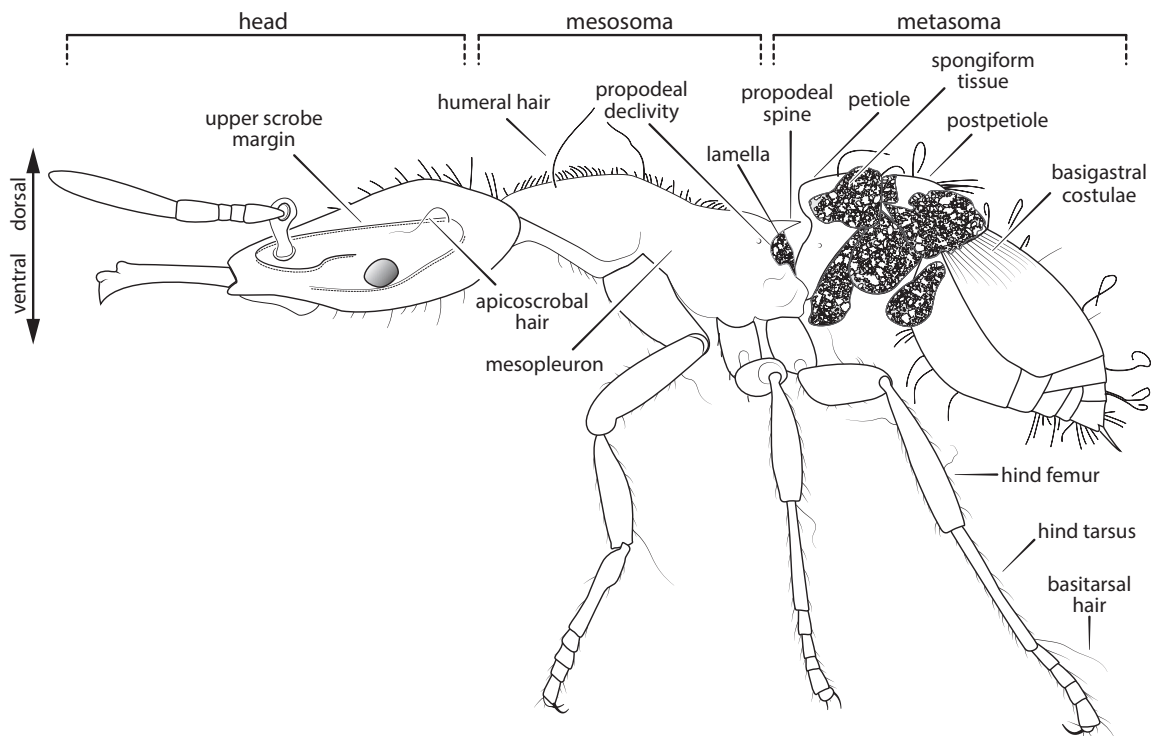   = *S. santschii* Forel

Fig. 2. Taxonomic characters in profile view

= *S. silvestriana* Wheeler
= *S. simillima* Emery
= *S. vitiensis* Mann
= *S. williamsi* Wheeler
S. nidifex Mann
S. oasis, **n. sp.**
S. panaulax Bolton
S. parzival, **n. sp.**
S. praefecta Bolton
S. rogeri Emery
= *S. incisa* Godfrey
= *S. sulfurea* Santschi
S. scelesta Mann

S. sulcata Bolton
S. trauma (Bolton)
S. tumida Bolton

Diagnosis of *Strumigenys* worker caste among Fijian ants
Small to minute. Head shape triangular. Antennae 6-segmented. Antennal club 2-segmented. Eyes located on lower margin of antennal scrobes. Mandibles either linear and tipped with apical fork or triangular and armed with numerous denticles. Propodeum armed with spines or teeth. Waist 2-segmented. Spongiform tissue attached to at least some portion of waist. Hairs appearing flagellate or spatulate on at least some portion of head or body.

Key to worker caste of Fijian *Strumigenys*
Refer to Figs. 2–5 for morphological terms used in the diagnostic key. Specific character states referred to in the key are presented in Fig. 6.

1. Mandibles triangular and armed with denticles (Fig. 6A) 2
– Mandibles linear and armed with an apical fork (Fig. 6B–F) 3
2. Dorsal surface of head covered by short appressed spatulate hairs (Fig. 5B, Fig. 8K). Pronotal humeral hairs present (Fig. 6R, Fig. 10T). Propodeal declivity lacking a broad and conspicuous spongiform lamella (Fig. 6V, Fig. 10S). Dorsal surfaces of mesosoma and petiole punctate (Fig. 10T) .... ***S. trauma***
– Dorsal surface of head not covered by short appressed spatulate hairs, hairs thin and simple (Fig. 5A, C, Fig. 8A). Pronotal humeral hairs absent (Fig. 6S). Propodeal declivity equipped with a broad and conspicuous spongiform lamella (Fig. 6W, Fig. 10A). Dorsal surfaces of mesosoma and petiole completely polished (Fig. 10B) .....***S. membranifera*** (introduced)
3. Preapical dentition of each mandible with two preapical teeth (Fig. 6F, Fig. 8H). Ventrolateral margin of head immediately in front of the eye with an abrupt and very conspicuous preocular notch or indentation (Fig. 6G) .... ***S. rogeri*** (introduced)
– Preapical dentition of each mandible either absent or with a single tooth (Fig. 6E) or denticle (Fig. 6C). Ventrolateral margin
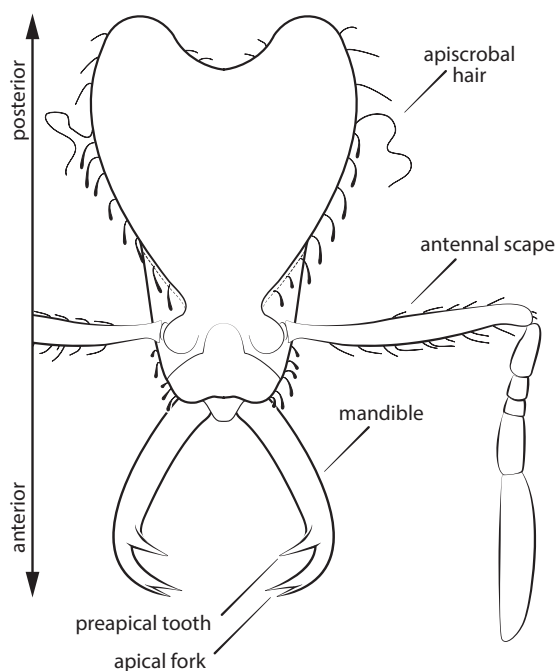

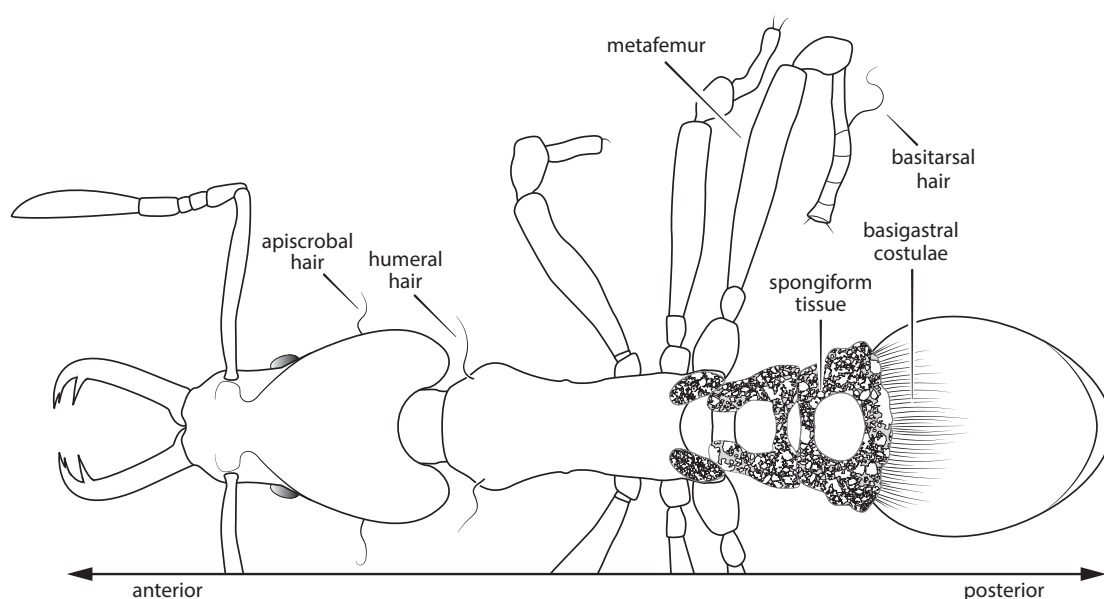**Fig. 3.** Taxonomic characters in full face view

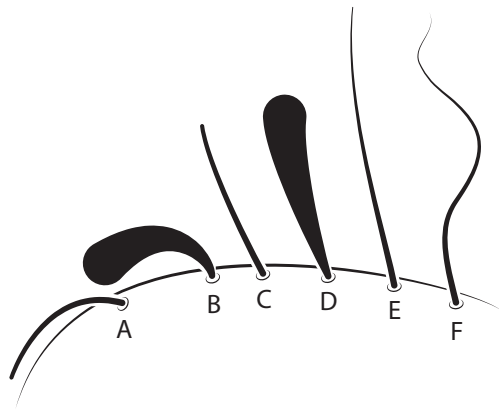**Fig. 4.** Taxonomic characters in dorsal view

Fig. 5. Types of hairs (A–E); (A) appressed simple, (B) appressed spatulate, (C) erect simple, (D) erect spatulate, (E) filiform, (F) flagellate

very conspicuous preocular notch or indentation (Fig. 6H) 4

4.   Dorsal (outer) surface of hind basitarsus with one or more freely projecting filiform (Fig. 5E) or flagellate (Fig. 5F) hairs that are very long and suberect to erect (Fig. 6P); this specialized pilosity may also be present on the middle basitarsus and the middle and hind tibiae (Fig. 10W) 5

–   Dorsal (outer) surface of the middle and hind basitarsi and tibiae lacking freely projecting long filiform or flagellate hairs (Fig. 6Q); any pilosity present is simple to spatulate and usually decumbent to appressed (Fig. 5A, B) 14

5.   First gastral tergite entirely covered with fine dense longitudinal sulcate sculpture (Fig. 6Z); no other form of sculpture present on sclerite 6

–   First gastral tergite not entirely covered with longitudinal sulcate sculpture; tergite usually with basigastral costulae that may extend up to half the length of the sclerite, which is usually unsculptured posteriorly (Fig. 6AA); occasionally tergite entirely smooth or with another form of sculpture distal of the basigastral costulae...7

6.   Dorsum of pronotum and petiole obliquely costulate-rugulose (Fig. 10H)..*S. panaulax*

–   Dorsum of pronotum and petiole longitudinally and irregularly rugoreticulate (Fig. 10J) ....*S. parzival*

7.   With mesosoma in profile the propodeal declivity equipped with a broad and conspicuous cuticular or spongiform lamella (Fig. 6W); the propodeal tooth may be replaced by the lamella or completely buried in the lamella, or the lamella may subtend the ventral margin of the tooth for most or all of its length; posterior (free) margin of lamella may be convex, straight or irregular but it is not narrowly concave, nor is it close to and parallel with the edge of the declivity 8

–   With mesosoma in profile the propodeal declivity equipped with a simple carina or at most a narrow cuticular spongiform flange (Fig. 6V); carina or narrow flange does not subtend the ventral margin of the tooth for most or all of its length; posterior (free) margin of carina or narrow flange concave, close to and parallel with the edge of the declivity 13

8.   With head in full-face view the upper scrobe margin with two or more flagellate or filiform hairs that freely project laterally (Fig. 6I, J); at least with one in apicoscrobal position and another anterior to this (dorsolateral margin of posterolateral lobe to apex of scrobe may have additional laterally projecting hairs) 9

–   With head in full-face view the upper scrobe margin usually with a single hair that freely projects laterally, in apicoscrobal position; this hair may be flagellate (Fig. 6K), filiform, or short and stiff (Fig. 6L); sometimes lacking a hair in this position (Fig. 6M) (dorsolateral margin of posterolateral lobe to apex of scrobe may have laterally projecting hairs) 10

9.   Freely projecting filamentous hairs present along entire lateral margin of head from posterolateral lobe to antennal insertions (Fig. 6I, Fig. 7A). Cephalic and pronotal surfaces smooth with large and deep irregular pits (Fig. 7A, Fig. 9B). First gastral segment lacking any sculpturing the entire length of the tergite (Fig. 9B) ....*S. anorak*

–   Freely projecting filamentous hairs lacking between the apicoscrobal hair and eye level (Fig. 6J, Fig. 7B). Cephalic and pronotal surfaces reticulate-punctate, lacking large irregular pits (Fig. 7E, Fig. 9J). First gastral segment with basigastral costulae distinctly longer than the length of the postpetiolar disc (Fig. 9J) .... *S. chernovi*

10. With mesosoma in profile dorsum of pronotum usually with one additional pair of hairs equal to the length of the humeral hair (Fig. 6X); rarely with more than one pair 11

–   With mesosoma in profile dorsum of pronotum lacking additional hairs equal to the length of the humeral hair (Fig. 6Y) 12

11. Eye composed of single facet (Fig. 9S) ....*S. gunter*

–   Eye composed of four or more facets (Fig. 9U) ....*S. jepsoni*

12. Apicoscrobal hair present and long, filiform or flagellate; this hair very different in form and length from any other on the margin both anterior and posterior to it (Fig. 6K). In profile dorsal surfaces of mesosoma, metasoma and gaster with long flagellate hairs (Fig. 6BB) ....*S. godeffroyi*

–   Apicoscrobal hair absent; entire margin with a dense row of uniformly shaped small curved hairs (Fig. 6M). In profile dorsal surfaces of mesosoma, metasoma and gaster lacking long flagellate hairs (Fig. 6CC) .... *S. scelesta*

13. With head in full-face view the upper scrobe margin with two or more flagellate or filiform hairs that freely project laterally (Fig. 7F); at least with one in apicoscrobal position and another anterior to this (dorsolateral margin of posterolateral lobe to apex of scrobe may have additional laterally projecting hairs) ....*S. daithma*

–   With head in full-face view the upper scrobe margin usually with a single flagellate hair that freely projects laterally; laterally projecting hairs also occur on dorsolateral margin of posterolateral lobe to apex. Refer to labeled structures in Fig. 2 for location of upper scrobe margin and apicoscrobal hair ....*S. ekasura*

14. Fully closed mandible in full-face view comparatively short and very broad proximally and strikingly tapered distally (Fig. 6D), not linear or curvilinear. Outer margin of mandible flared outwards or strongly convex prebasally, the mandible not straight, not evenly convex, not evenly bowed outwards 15

–   Fully closed mandible in full-face view comparatively long and usually obviously linear or curvilinear, sometimes slightly increasing in width towards the base (Fig. 6B, C). Outer margin of mandible not flared outwards or strongly convex prebasally, mandible straight, evenly convex, or evenly bowed outwards 16

15. Posteromedian margin of head with single deep circular puncture (Fig. 8D). With mesosoma in profile the propodeal declivity equipped with a broad and conspicuous spongiform
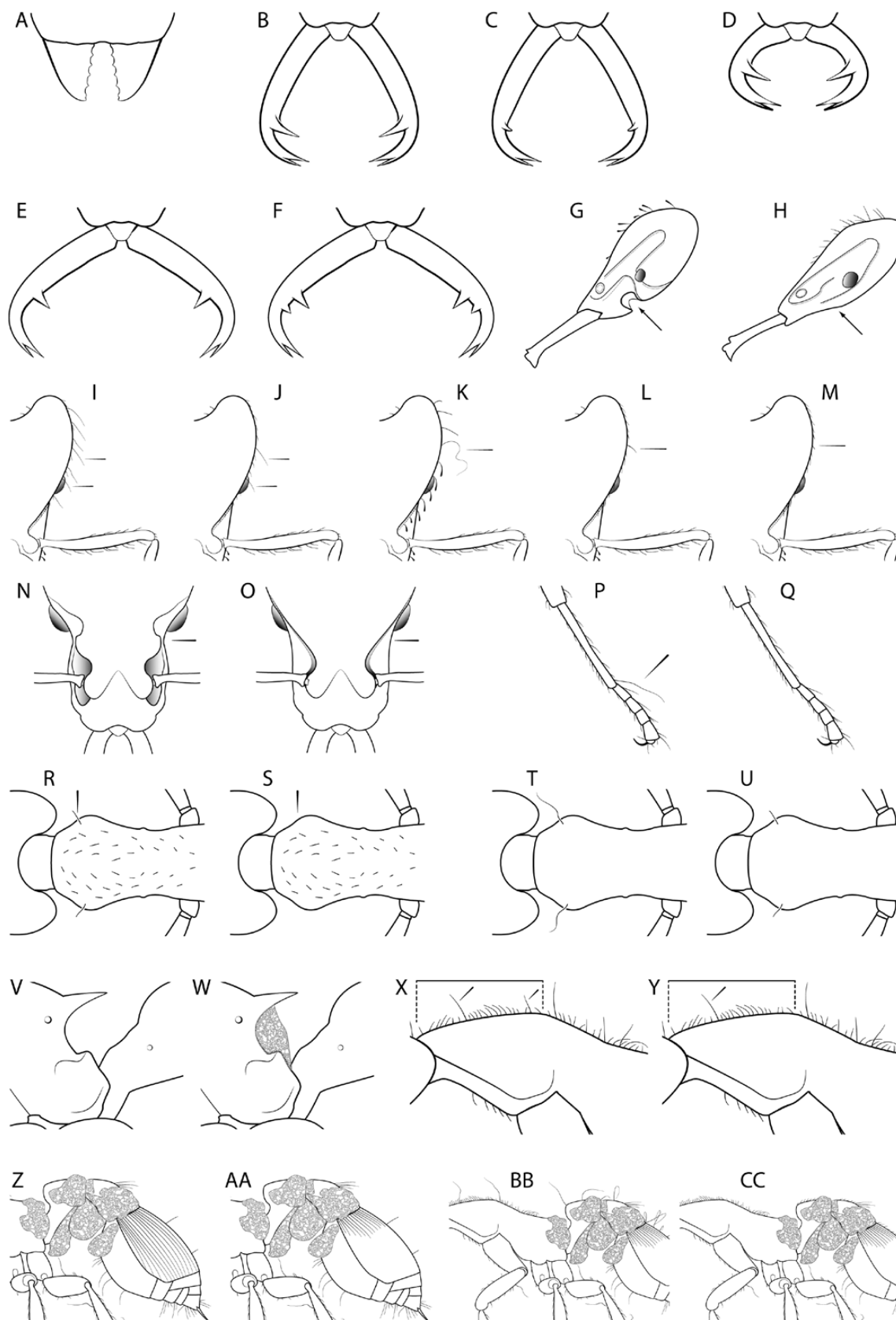
Fig. 6. Taxonomic characters used in identification key (A–CC)

lamella (Fig. 6W). Dense tuft of white filamentous hairs arising from the lateral promesonotal border above the procoxae (Fig. 10E). Dorsum of mesosoma with abundant long white erect hairs (Fig. 10E) .... *S. oasis*

– Posteromedian margin of head lacking single deep circular puncture (Fig. 7D). Dense tuft of white filamentous hairs lacking from the lateral promesonotal border above the procoxae (Fig. 9G). With mesosoma in profile the propodeal declivity lacking a conspicuous spongiform lamella (Fig. 6V). Dorsum of mesosoma lacking abundant long white erect hairs (Fig. 9G) ....*S. basiliska*

16. Pronotal humeral hair absent (Fig. 6S) 17
– Pronotal humeral hair present (Fig. 6R) 18

17. Dorsum of pronotum coarsely and deeply longitudinally sulcate, with a ploughed appearance (Fig. 10R). Disc of postpetiole longitudinally sulcate, sulci narrower and finer than on pronotum (Fig. 10R). Cephalic dorsum coarsely longitudinally rugose (Fig. 8J). Ventral spongiform curtain of petiole narrow, at maximum only a fraction the depth of the peduncle (Fig. 10Q) ....*S. sulcata*

– Dorsum of pronotum densely reticulate-punctate (Fig. 10L). Disc of postpetiole weakly rugulose (Fig. 10L). Cephalic dorsum sharply and densely reticulate-punctate (Fig. 8G). Ventral spongiform curtain of petiole deep, at maximum at least equal to the depth of the peduncle (Fig. 10K) ....
.... *S. praefecta*

18. In full-face view, sides of head immediately in front of the eye with an abrupt and very conspicuous indentation (Fig. 6N). Large species (HW > 0.80 mm) 19
– In full-face view, sides of head immediately in front of the eye lacking an abrupt and very conspicuous indentation (Fig. 6O). Small species (HW < 0.70 mm) 20

19. Sculpture on first gastral tergite consisting of basigastral costulae restricted to less than a quarter of the length of the tergite, remainder the tergite strongly polished and shiny (Fig. 10C, D) ....*S. nidifex*

– Sculpture on first gastral tergite consisting of basigastral costulae restricted to basal half of the tergite and strongly reticulate-punctate ground sculpture covering the entire tergite (Fig. 9; Fig. 10E, F) ....*S. avatar*

20. Preapical dentition of mandible a stout tooth/denticle that is distinctly shorter than the width of the mandible at the point where it arises (Fig. 6C; Fig. 8L); preapical tooth never as long as the maximum width of the mandible. Mesopleuron and procoxa reticulate-punctate (Fig. 10U) .... *S. tumida*

– Preapical dentition of mandible a slender spiniform tooth that is always longer than the width of the mandible at the point where it arises (Fig. 6B); preapical tooth usually at least as long as the maximum width of the mandible. Mesopleuron and procoxa smooth and shiny 21

21. Apicoscrobal and pronotal humeri hairs flagellate (Fig. 7H; Fig. 9O, P). Pronotal dorsum lacking erect hairs in addition to the humeral pair (Fig. 6Y) .... *S. frivola*

– Apicoscrobal and pronotal humeri hairs simple. Pronotal dorsum with erect hairs in addition to the humeral pair (Fig. 6X) 22

22. Hairs on dorsal surface of head, mesosoma and metasoma short, thick and subdecumbent (Fig. 9C). In full face view eyes mostly shielded by lateral head margins (Fig. 7B) ....
.... *S. artemis*

– Hairs on dorsal surface of head, mesosoma and metasoma long, fine and erect (Fig. 9W). In full face view eyes visible, not shielded by lateral head margins (Fig. 7L) ....*S. mailei*

Species accounts

S. anorak n. sp.

(Fig. 7A; Fig. 9A, B; Fig. 11; Fig. 26, Model 1)

(Zoobank LSID: urn:lsid:zoobank.org:act:65D7817A-EAA1-4A8F-9A87-992C2C141829)

HOLOTYPE. Fiji, Viti Levu, Ra Prov., 7.5 km NE Vunisea Village, 2003-07-14, 300 m, –17.4833° 178.1430°, small forest fragment, sifted litter, A. Rakabula (worker, dry pinned, BPBM, specimen code CASENT0186900).
= *Strumigenys* sp. FJ18 (Sarnat and Economo 2012: 136, pl. 140)

Cybertype. Volumetric raw data (in DICOM format) of the physical holotype (CASENT0186900) is deposited at Dryad (https://doi.org/10.5061/dryad.1f9d55b/1) and can be freely accessed as virtual representation of the type. In addition to the cybertype data at Dryad, we also provide a freely accessible 3D surface model of the holotype at Sketchfab (https://skfb.ly/6vsIH).

Worker. Measurements (*n* = 3): TL 3.18–3.40 mm, HL 0.79–0.87 mm, HW 0.54–0.59 mm, CI 68, MdL 0.35–0.36 mm, MI 41–45, SL 0.51–0.57 mm, SI 96, PW 0.37–0.40 mm, PI 68, FL 0.62–0.68 mm, FI 115, EL 0.08–0.09 mm. Color a polished reddish-brown with yellowish-brown appendages. Mandible long and linear with one preapical tooth; preapical tooth approximately as long as maximum mandible width. Dorsolateral head margin with abundant laterally projecting filiform and occasionally flagellate hairs. Apicoscrobal hair flagellate. Upper scrobe margin anterior to apicoscrobal hair with filiform hairs. Cephalic dorsum irregularly reticulate-punctate. Ground pilosity of cephalic dorsum simple and long. Pronotal humeral hair flagellate. Promesonotal dorsum with abundant projecting filiform apically curved hairs; mesonotum with at least one pair of longer flagellate hairs. Promesonotal dorsum and propodeal dorsum smooth and marked by laterally by deep and occasionally overlapping spongiform filled pits of irregular size and shape from small and circular to large and ovoid. Side of promesonotum smooth and marked with pits similar to those of dorsal surface. Mesopleuron, metapleuron and side of propodeum glassy smooth. Propodeal tooth short, narrowly triangular, subtended by a broad lamella with a convex posterior margin. Dorsal and ventral surfaces of hind femur with abundant erect filiform and subflagellate hairs. Dorsal surface of hind tibia with one filiform hair on basal portion and one subflagellate hair on apical portion. Dorsal surface of hind tarsus with three flagellate hairs. With petiole node in profile the dorsum of the node much longer than its short oblique anterior face; lateral spongiform lobe small; restricted to posterior margin of node. Dorsum of petiole node highly polished with scattered irregular shaped pits. Disc of postpetiole glassy smooth. Ventral lobe of postpetiole spongiform. First gastral tergite with erect flagellate hairs and long ground pilosity. Basigastral sculpture entirely absent.

Strumigenys anorak is a relatively large and highly distinctive rich reddish brown species with abundant flagellate and filiform hairs on its dorsal surfaces, a unique sculpture characterized by a smooth integument interrupted by deep irregularly sized and shaped pits, and the presence of a broad and conspicuous propodeal lamella. Additional characters for separating *S. anorak* from similar Fijian species are given in the notes for *S. daithma*. The species is represented by three specimens, two from Gau and one from Viti Levu, all between 400 and 475 meters and collected from extracted leaf litter.

Etymology: *Anorak* refers to the online avatar of James Donovan Halliday, creator of the virtual reality world OASIS, in the fictional work *Ready Player One* (Cline 2011). The name is a noun in apposition and thus invariable.

S. artemis n. sp.

(Fig. 7B; Fig. 9C, D; Fig. 12; Fig. 26, Model 2)

(Zoobank LSID: urn:lsid:zoobank.org:act:4178E8F2-8418-491F-A419-49A573BB8D46)

HOLOTYPE. Fiji, Viti Levu, Savarua Creek 8.0 km W Colo-i-Suva Village, 2003-02-24, 200m, −18.0589° 178.4420°, primary rainforest, sifted litter, A. Tabutabu (worker, dry pinned, BPBM, specimen code CASENT0184980).
= *Strumigenys* sp. FJ13 (Sarnat and Economo 2012: 135, pl.137)
= *Strumigenys* sp. FJ17 (Sarnat and Economo 2012: 136, pl.139)

Virtual dataset. Volumetric raw data (in DICOM format) of the nontype specimen (CASENT0186982) is deposited at Dryad (https://doi.org/10.5061/dryad.1f9d55b/2) and can be freely accessed as virtual representation of the species. In addition to the data at Dryad, we also provide a freely accessible 3D surface model at Sketchfab (https://skfb.ly/6v8OR).

Worker. Measurements (*n* = 11): TL 1.92–2.38 mm, HL 0.46–0.59 mm, HW 0.36–0.45 mm, CI 73–79, MdL 0.20–0.23 mm, MI 37–48, SL 0.28–0.39 mm, SI 70–77, PW 0.21–0.25 mm, PI 55–62, FL 0.28–0.39 mm, FI 78–94, EL 0.21–0.25 mm. Color a dull uniform yellowish brown. Mandibles long and linear with one preapical tooth; preapical tooth length approximate to maximum mandible
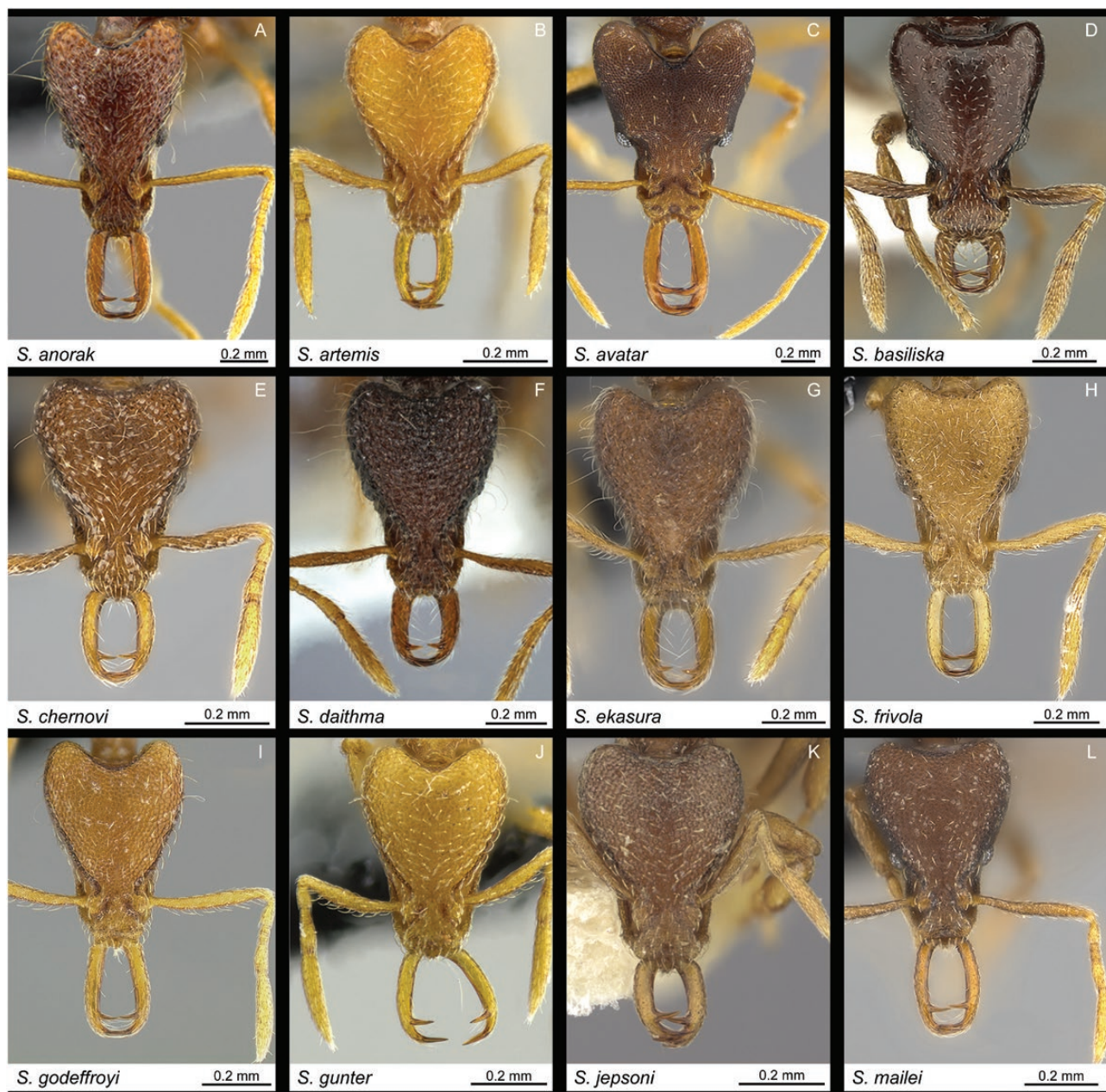
Fig. 7. Worker caste of Fijian *Strumigenys* species in full face view (A–L). (A) *S. anorak* n. sp., holotype, CASENT0186900; (B) *S. artemis* n. sp., holotype, CASENT0184980; (C) *S. avatar*, n. sp., holotype, CASENT0185902; (D) *S. basiliska*, paratype, CASENT0013153; (E) *S. chernovi*, CASENT0184914; (F) *S. daithma*, ANIC32017716; (G) *S. ekasura*, CASENT0184678; (H) *S. frivola*, paratype, BMNH(E) 1014221; (I) *S. godeffroyi*, CASENT0171155; (J) *S. gunter* n. sp., holotype, CASENT0184984; (K) *S. jepsoni*, syntype, CASENT0235852; (L) *S. mailei*, CASENT0186741.
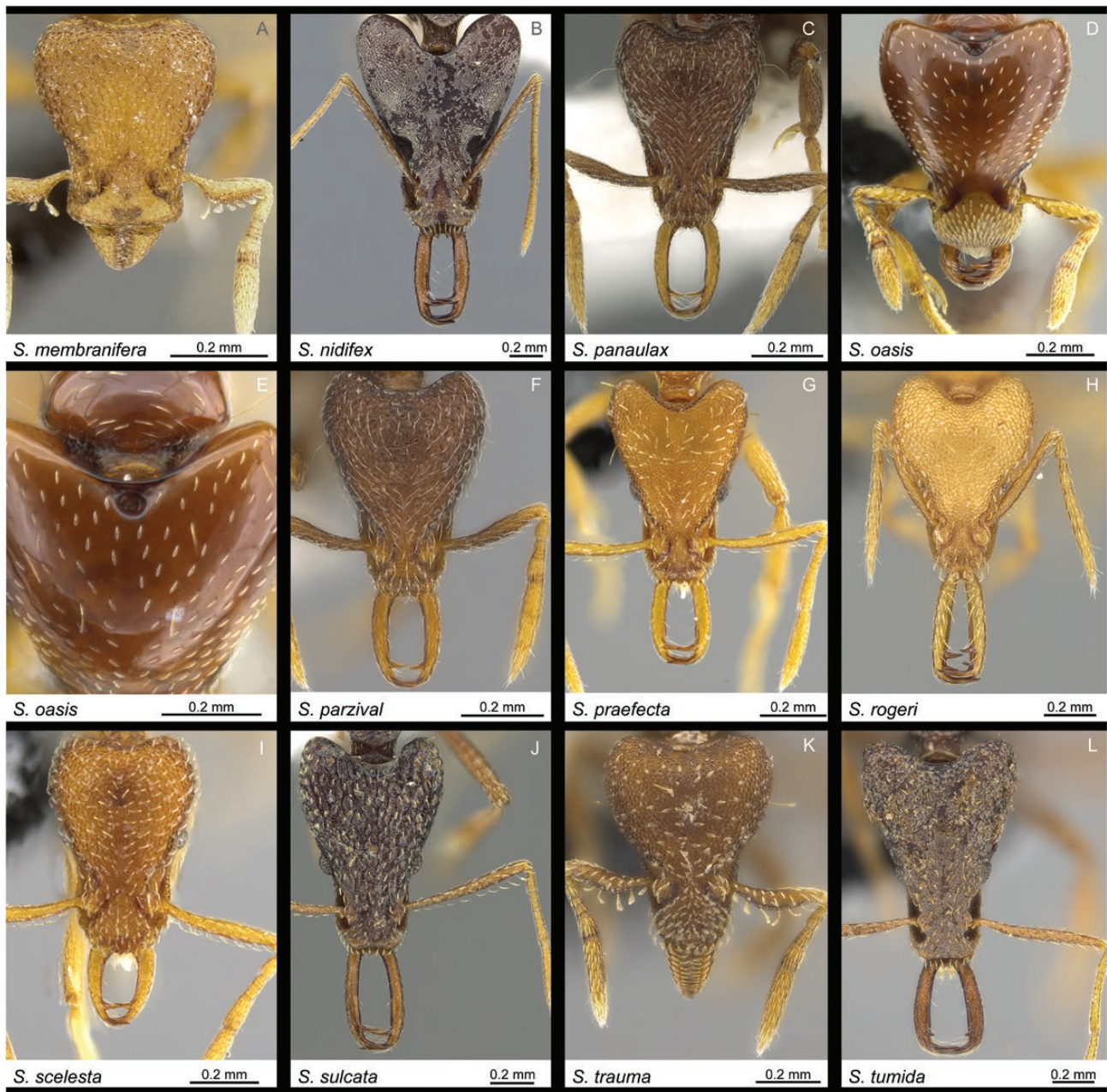
Fig. 8. Worker caste of Fijian *Strumigenys* species in full face view (A–L). (A) *S. membranifera*, CASENT0171134, (B) *S. nidifex*, CASENT0914852; (C) *S. oasis* n. sp., holotype, CASENT0185751; (D) *S. oasis* close-up of posterior head margin; (E) *S. panaulax*, paratype, BMNH(E) 1014216; (F) *S. parzival* n. sp., holotype, CASENT0186960; (G) *S. praefecta*, CASENT0186986; (H) *S. rogeri*, CASENT0767610; (I) *S. scelesta*, CASENT0186833; (J) *S. sulcata*, paratype, CASENT0013152; (K) *S. trauma*, CASENT0184729; (L) *S. tumida*, CASENT0186506

width. Apicoscrobal hair short and simple, weakly projecting laterally but not filiform or flagellate. Cephalic dorsum uniformly reticulate-punctate. Ground pilosity of cephalic dorsum short, simple, strongly curved. Pronotal humeral hairs short and simple. Promesonotal dorsum with short curved ground pilosity; lacking long filiform or flagellate hairs. Promesonotal dorsum and sides longitudinally striate to reticulate-punctate. Propodeal dorsum uniformly reticulate-punctate. Mesopleuron, metapleuron and side of propodeum mostly smooth. Propodeal tooth short, narrowly triangular. Lamellae attending the propodeal spines vary from thin and parallel to the declivity, to wider and not paralleling the declivity. Legs entirely lacking projecting filiform to flagellate hairs. Petiolar node in profile evenly convex with similar anterior and posterior

faces; lateral spongiform lobe small; restricted to posterior margin of node. Dorsum of petiole strongly reticulate-punctate. Postpetiolar disc weakly reticulate-punctate. Ventral lobe of postpetiole spongiform. First gastral tergite with erect flagellate hairs and long ground pilosity. Basigastral sculpturing is conspicuously longer than the length of the postpetiolar disc.

Strumigenys artemis is a small, dull yellowish-brown species with strongly reduced pilosity. The apicoscrobal and humeral hairs are short and simple, and the legs lack erect hairs entirely. The Fijian species most resembling *S. artemis* are *S. jepsoni* and *S. mailei*. Whereas *S. artemis* and *S. mailei* have relatively short and simple apicoscrobal and humeral hairs, those of *S. jepsoni* are long and flagellate. *Strumigenys artemis* is distinguished from

Fig. 9. Worker caste of Fijian *Strumigenys* species in profile and dorsal views (A–X). (A B) *S. anorak* n. sp., holotype, CASENT0186900; (C, D) *S. artemis* n. sp., holotype, CASENT0184980; (E, F) *S. avatar*, holotype, CASENT0185902; (G, H) *S. basiliska*, paratype, CASENT0013153; (I, J) *S. chernovi*, CASENT0184914; (K, L) *S. daithma*, ANIC32017716; (M, N) *S. ekasura*, CASENT0184678; (O, P) *S. frivola*, paratype, BMNH(E)1014221; (Q, R) *S. godeffroyi*, CASENT0171155; (S,T) *S. gunter* n. sp., holotype, CASENT0184984; (U, V) *S. jepsoni*, syntype, CASENT0235852; (W, X) *S. mailei*, CASENT0186741.

S. mailei by fewer number of erect hairs on all dorsal surfaces and the also by the position of the eyes which are obscured by the lateral cephalic margins in full face view. Moderate variation in size, sculpture and pilosity is observed across what we define

here as *Strumigenys artemis*. Sarnat and Economo (2012) originally treated this as two distinct species (*Strumigenys* sp. FJ13 and *Strumigenys* sp. FJ17). Closer examination reveals that none of the specimens treated as *Strumigenys* sp. FJ17 present flagellate

Fig. 10. Worker caste of Fijian *Strumigenys* species in profile and dorsal views (A–X). (A, B) *S. membranifera*, CASENT0171134; (C, D) *S. nidifex*, CASENT0914852; (E, F) *S. oasis* n. sp., holotype, CASENT0185751; (G, H) *S. panaulax*, paratype, BMNH(E)1014216; (I, J) *S. parzival* n. sp., holotype, CASENT0186960; (K, L) *S. praefecta*, CASENT0186986; (M, N) *S. rogeri*, CASENT0767610; (O, P) *S. scelesta*, CASENT0186833; Q, R) *S. sulcata*, paratype, CASENT0013152; S,T) *S. trauma*, CASENT0184729; (U, V) *S. tumida*, CASENT0186506; (W) freely projecting hairs on the middle tibia, middle tarsus, and basitarsus; (X) close-up profile of *S. oasis* mesosoma.

hairs on the legs, and the differences in sculpture and pilosity are not discrete enough to warrant separation of species. *Strumigenys artemis* is widespread, occurring even on the smaller islands in the archipelago.

Etymology: *Artemis* is the Latinized version of Art3mis, a famous gunter in the fictional work *Ready Player One* (Cline 2011). *Artemis* is also the Greek goddess of the hunt and is an apt name for a *Strumigenys* species. The name is a noun in apposition and thus invariable.
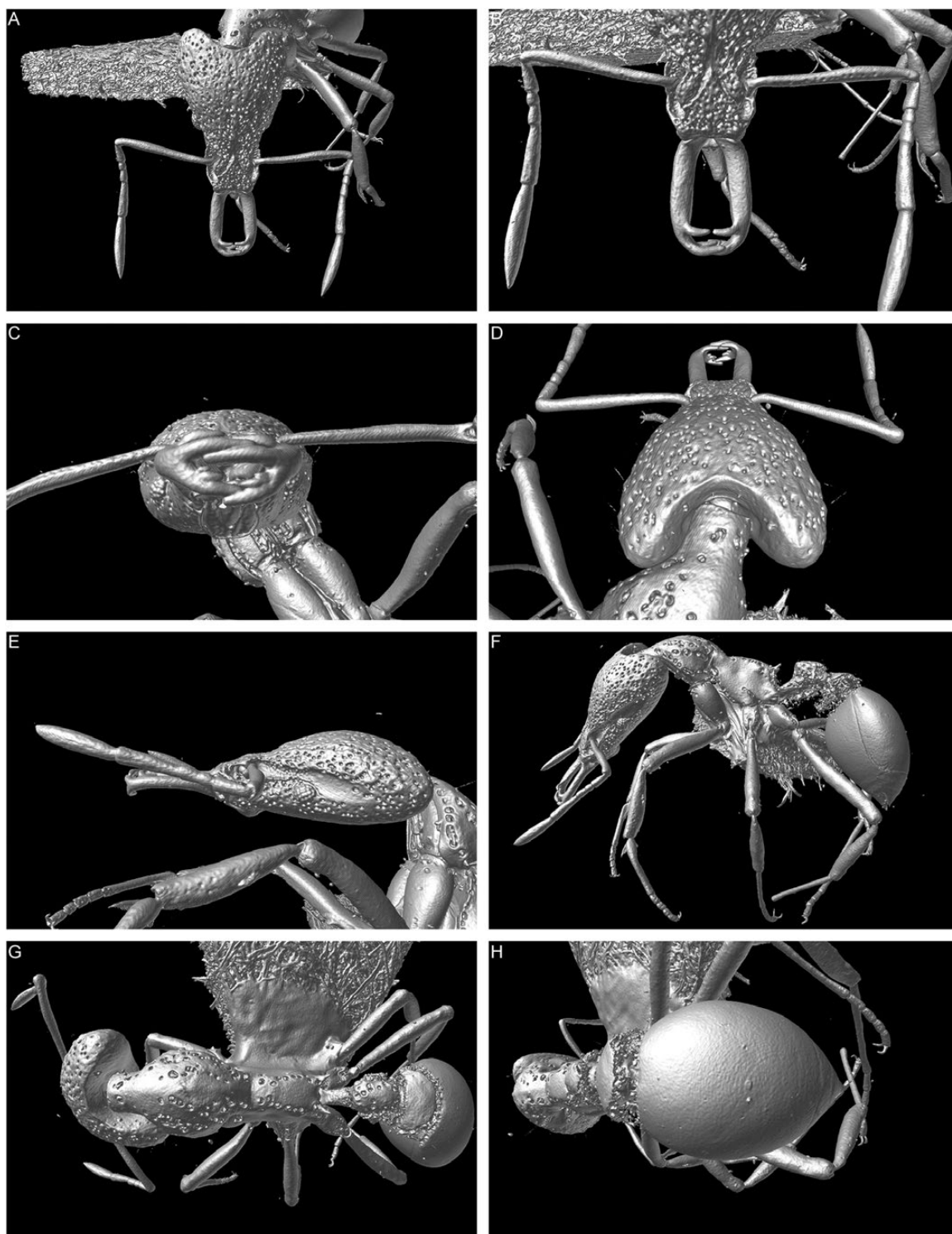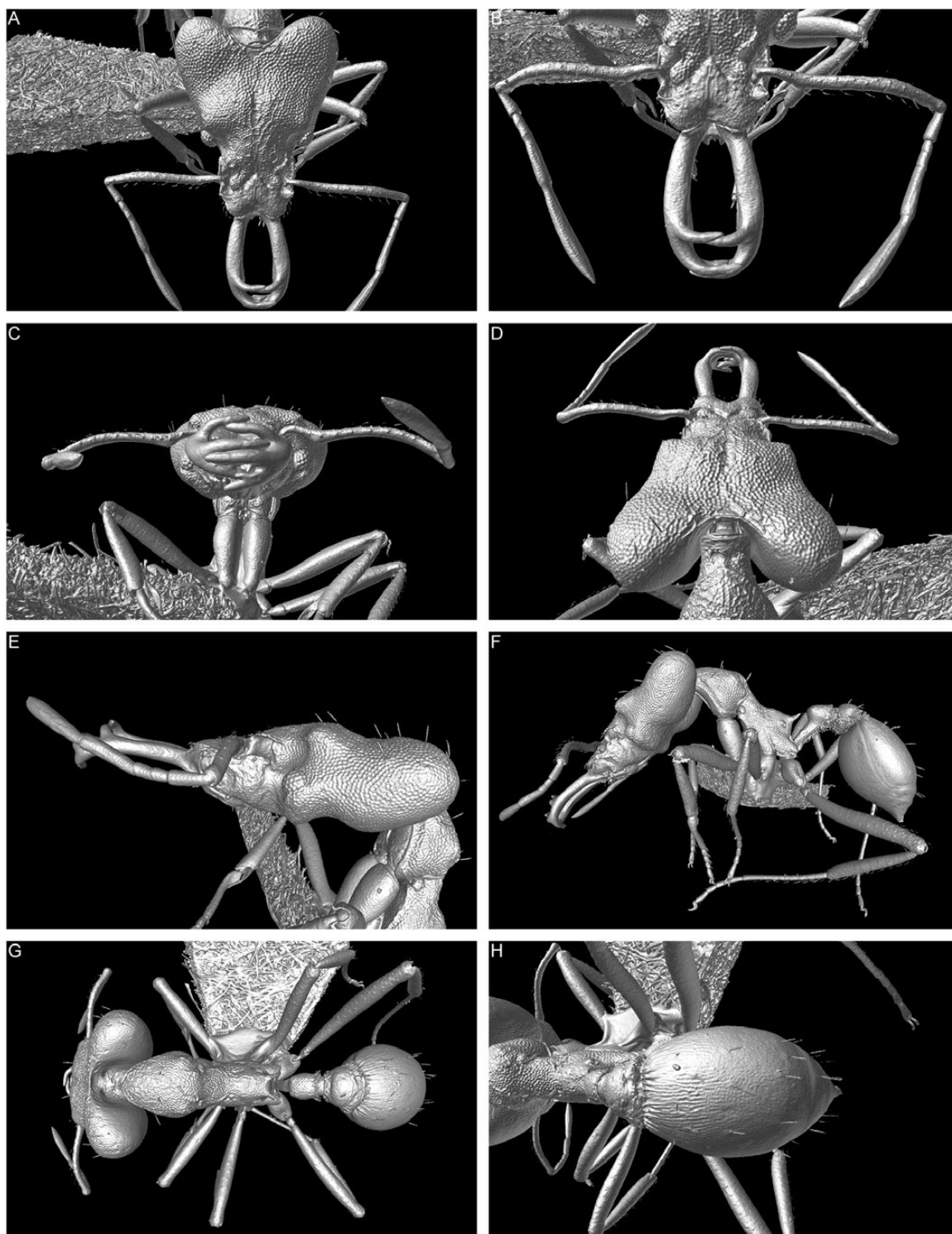
Fig. 11. [AR marker] Shaded surface display volume renderings of *Strumigenys anorak* n. sp. (CASENT0186900). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view. Scan in AR mode using Insects3D app to project 3D model.

S. avatar n. sp.

([Fig. 7C](#); [Fig. 10E](#), F; [Fig. 13](#); [Fig. 26](#), [Model](#) 3)

(Zoobank LSID: urn:lsid:zoobank.org:act:422C0FAD-AF1B-4C1A-92F6-DA2EEB93950B)

HOLOTYPE. Fiji, Viti Levu, Naitasiri, Mt. Naqaranibuluti, 1.3 km W Emperor Gold Mine Rest House, 2005-06-24, 1050m, −17.5694° 177.9700°, primary rainforest, nesting under stone, E.M. Sarnat, EMS2137 (worker, dry pinned, BPBM, specimen code CASENT0185902). PARATYPEs (same data as holotype): 1 dealate queen (CASENT0185537, USNM); 1 male (CASENT0185924, USNM), 1 male (CASENT0185658, USNM), 1 worker (CASENT0185710, USNM), 1 worker (CASENT0185928, USNM), 1 worker (CASENT0187698, MCZC, damaged), 1 worker (CASENT0187561, MCZC), 1 worker (CASENT0186464, MCZC).
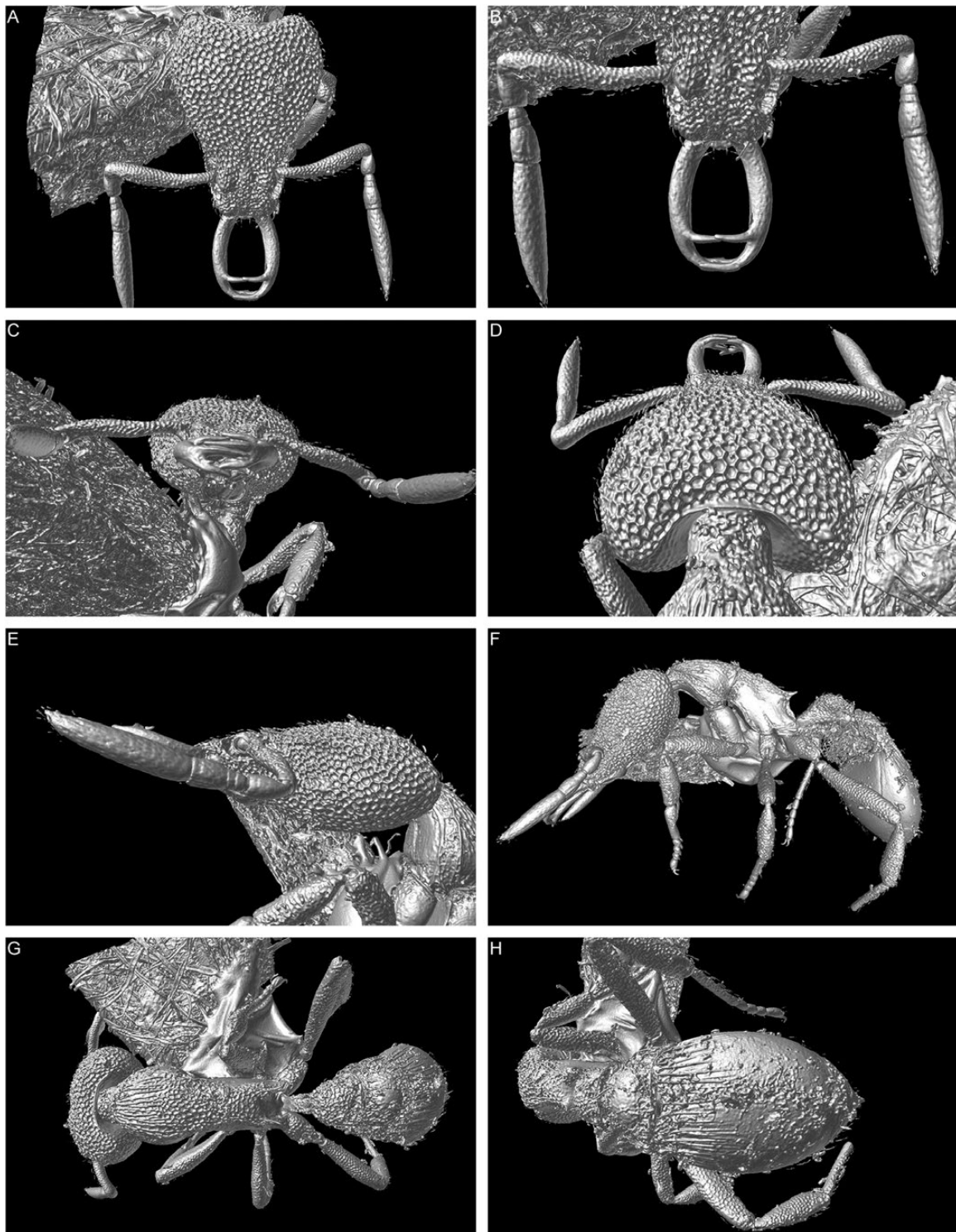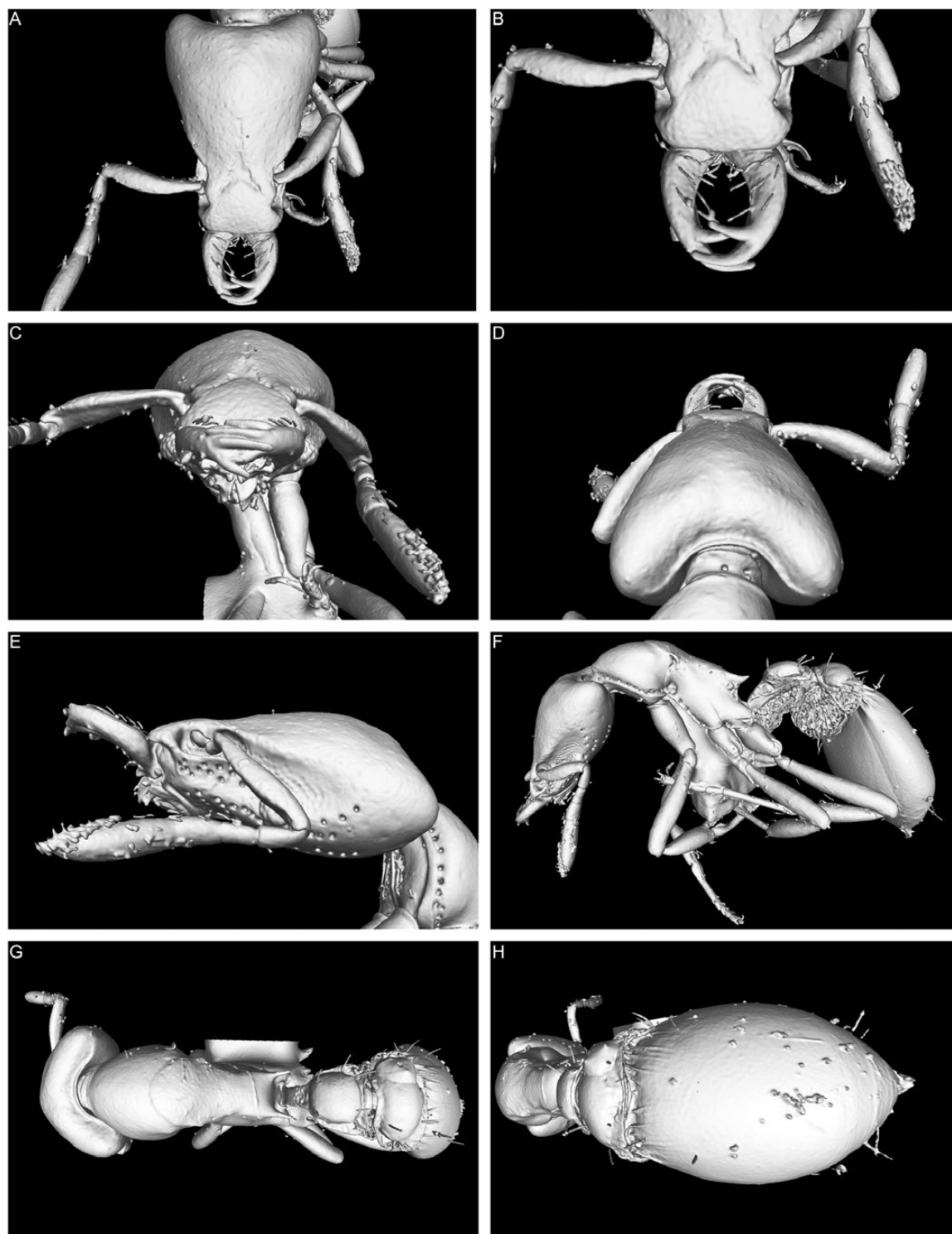
Fig. 12. [AR marker] Shaded surface display volume renderings of *Strumigenys artemis* n. sp. (CASENT0186982). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view. Scan in AR mode using Insects3D app to project 3D model.

= *Strumigenys* sp. FJ01 (Sarnat and Economo 2012: 135, pl. 136)

Cybertype. Volumetric raw data (in DICOM format) of the physical holotype (CASENT0185902) is deposited at Dryad (https://doi.org/10.5061/dryad.1f9d55b/3) and can be freely accessed as virtual representation of the type. In addition to the cybertype data at

Dryad, we also provide a freely accessible 3D surface model of the holotype at Sketchfab (https://skfb.ly/6v8Op).

Worker. Measurements (n = 6): TL 4.28–4.60 mm, HL 1.02–1.19 mm, HW 0.87–0.99 mm, CI 79–86, MdL 0.46–0.58 mm, MI 45–49, SL 0.89–1.01 mm, SI 74–83, PW 0.42–0.45 mm, PI 46–48, FL 0.89–1.01 mm, FI 99–107, EL 0.42–0.45 mm. Color dull dark

Fig. 13. [AR marker] Shaded surface display volume renderings of *Strumigenys avatar* n. sp. (CASENT0185902). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view. Scan in AR mode using Insects3D app to project 3D model.

reddish-brown with yellowish-brown appendages. Mandibles long and linear. Apical fork composed of two spiniform teeth and a single intercalary denticle. Single stoutly spiniform preapical tooth present close to the apicodorsal tooth. Cephalic dorsum uniformly reticulate-punctate; with five pairs of erect simple hairs on posterior margin and one pair close to the highest point of vertex. Antennal scapes very long. In full-face view, sides of head immediately in front of the eye with an abrupt and very conspicuous indentation. Vertex of head raised with dorsolateral margin mesad of eye formed into a knobby protuberance. Region of head between vertex and posterolateral lobes depressed. Scrobe absent behind level of eye. Pronotal humeral hairs simple, short and stiff. Two additional pairs
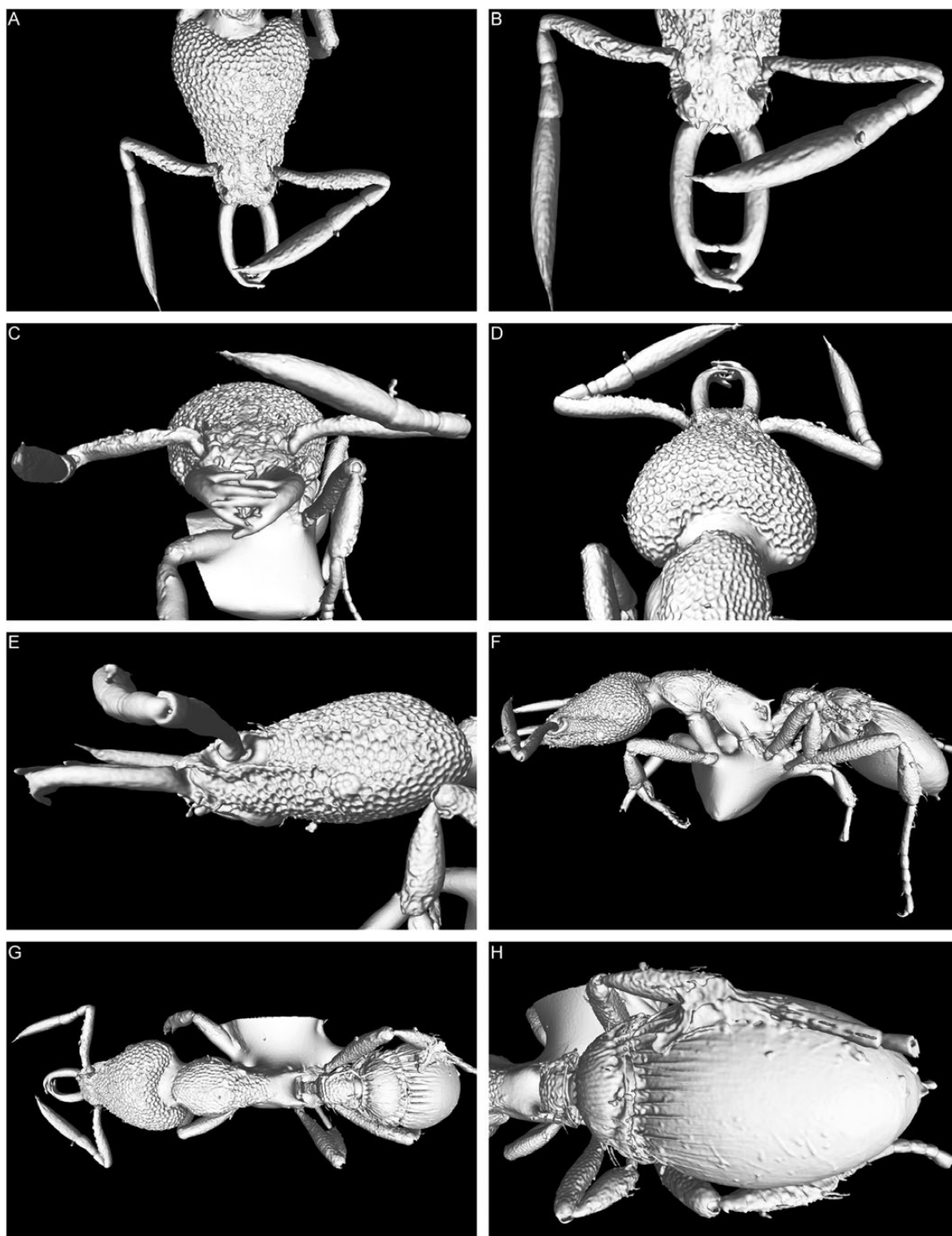
Fig. 14. Shaded surface display volume renderings of *Strumigenys basiliska* (CASENT0185655). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

of simple erect hairs present on promesonotum. Postpetiole with two pairs of erect hairs, first gastral segment with five pairs. Legs entirely lacking projecting hairs. Mesosoma, petiole, and postpetiole uniformly and finely reticulate-punctate on all surfaces. Propodeal teeth free; margin of declivity entirely lacking even a thin lamella. Petiole node in dorsal view conspicuously longer than broad. Spongiform appendages of waist segments reduced. On petiole present as a thin, narrow curtain subtending the ventral margin and

posterodorsal margin. Entire first tergite and sternite of gaster finely striate-punctate.

Strumigenys avatar is a large, long-limbed, dark reddish-brown species with a distinctive head shape. The only other Fijian species resembling *S. avatar* is its close and better-known relative *S. nidifex*. The two can be easily distinguished by the first gaster tergite and sternite. In *S. avatar*, these are entirely striate-punctate. In *S. nidifex*, sculpture is restricted to short basigastral costulae on the tergite.
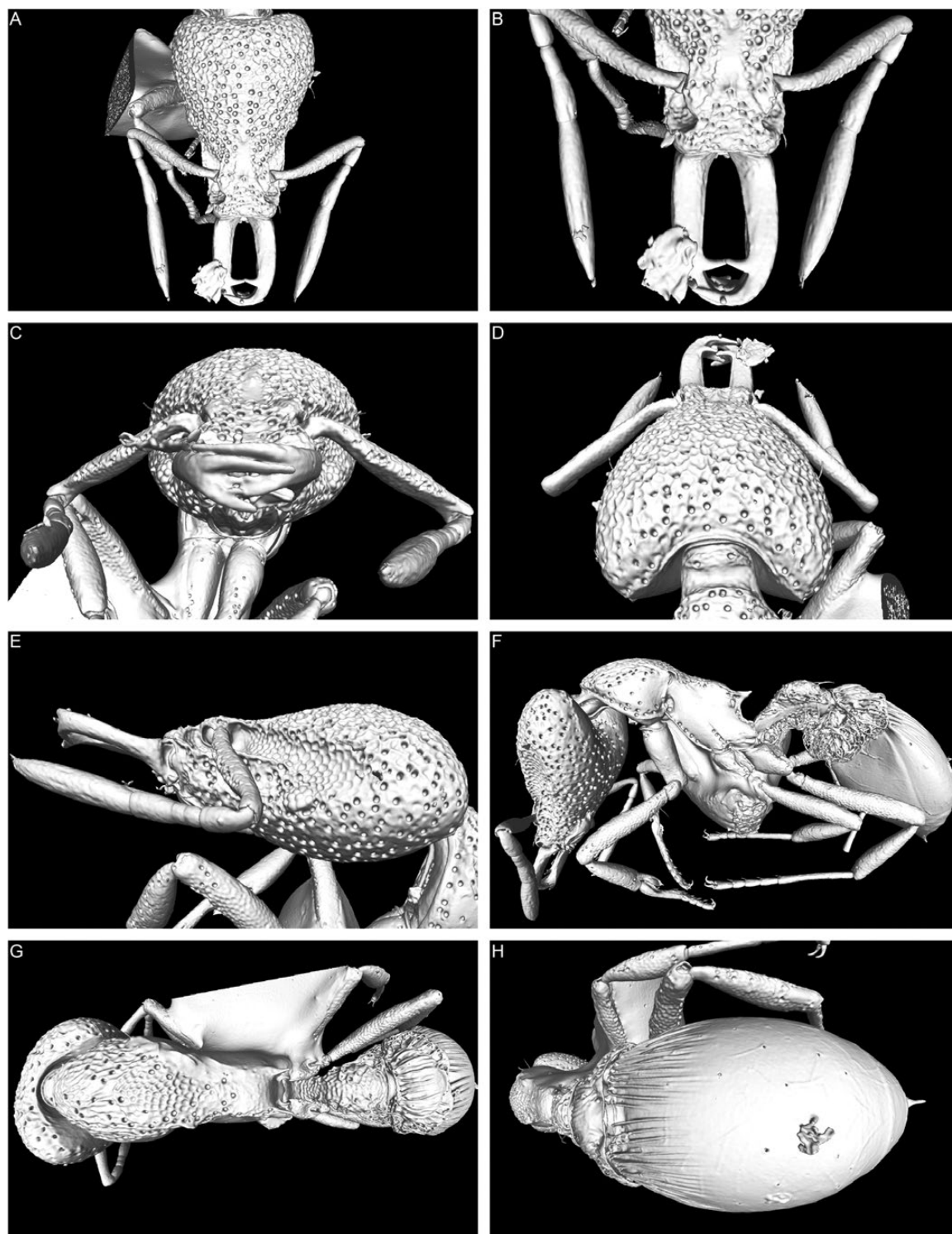
Fig. 15. Shaded surface display volume renderings of *Strumigenys chernovi* (CASENT0184909). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

Additional discussion of these two species is given under the notes of *S. nidifex*. *Strumigenys avatar* is known only from a single collection in the Nadarivatu area (Viti Levu), which is also the type locality of *S. nidifex*. The two are sympatric, which, together with the clear morphological differences, validates the distinction of two separate species.

Etymology: Avatar refers to the three-dimensional representation of OASIS users in the fictional work *Ready Player One* (Cline 2011). The name is a noun in apposition and thus invariable.

S. basiliska Bolton

(Fig. 7D; Fig. 9G, H; Fig. 14, Fig. 26)

basiliska. *Strumigenys basiliska* Bolton 2000: 750; worker described. Type locality: FIJI, Viti Levu, Nadarivatu Reserve, 11.vii.1987, QM Berlesate no. 775, 17.34°S, 177.57°E, 800 m., rainforest, sieved litter (G. Monteith). HOLOTYPE: worker
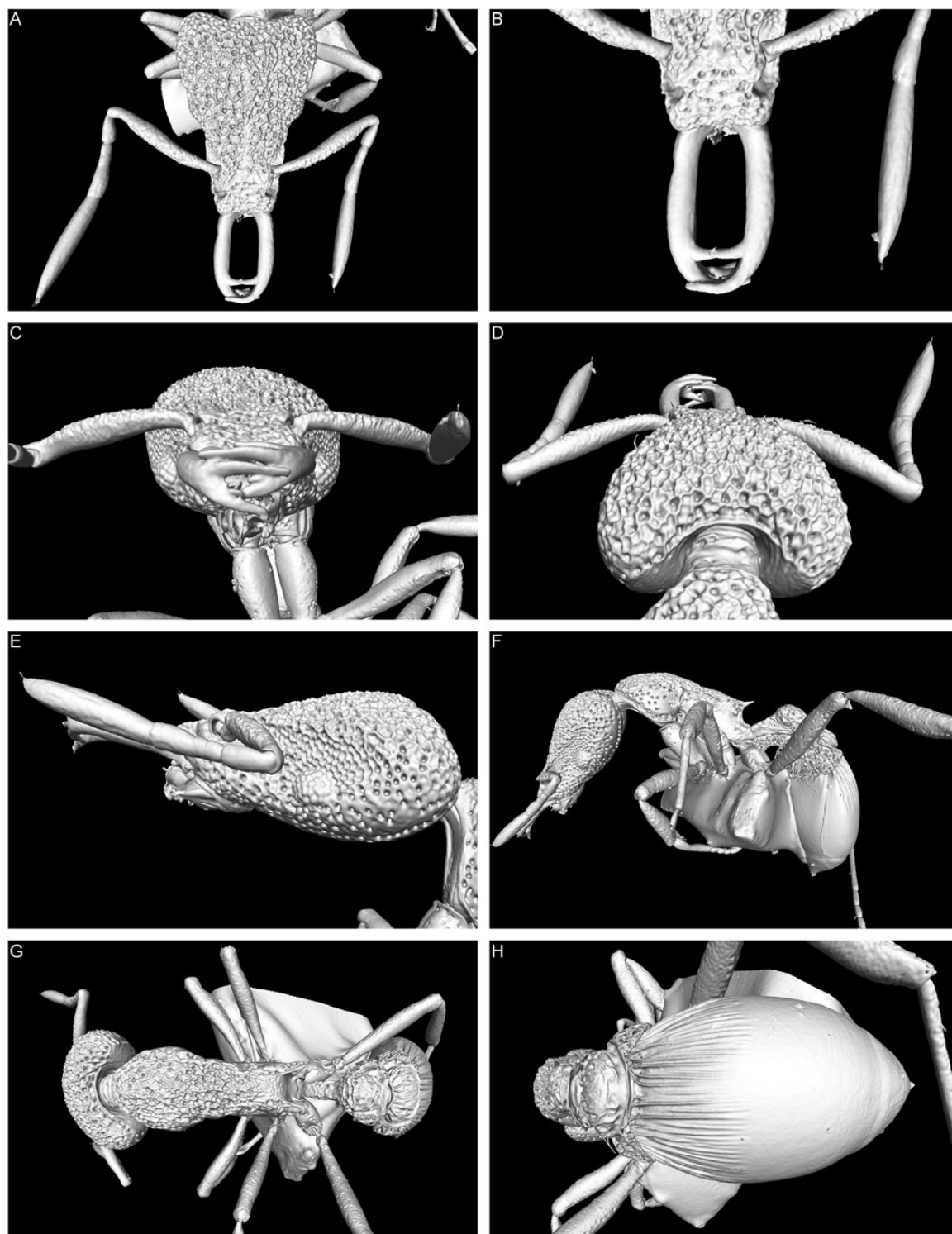
Fig. 16. Shaded surface display volume renderings of *Strumigenys ekasura* (CASENT0184622). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

(ANIC, examined). PARATYPEs: workers (ANIC, examined); workers (BMNH, examined). In Fiji (Sarnat and Economo 2012: 127, pl. 121).

Worker. Measurements (*n* = 3): TL 2.5–2.7, HL 0.64–0.68, HW 0.46–0.50, CI 72–74, MdL 0.18–0.20, MI 28–30, SL 0.32–0.33, SI 67–70, PW 0.29–0.32. *Strumigenys basiliska* is a distinctive species that can

be recognized by the highly polished dark reddish-brown color, reduced pilosity, short arcuate mandibles, and lack of propodeal lamellae. Although morphological variation of *S. basiliska* across the archipelago is largely congruent with geographic patterns (Sarnat and Economo 2012), genetic analysis suggests that these differences represent intraspecific variation across populations (Liu et al. in prep.). Bolton tentatively placed *S. basiliska* in the *biroi* group but admitted that the Fijian species
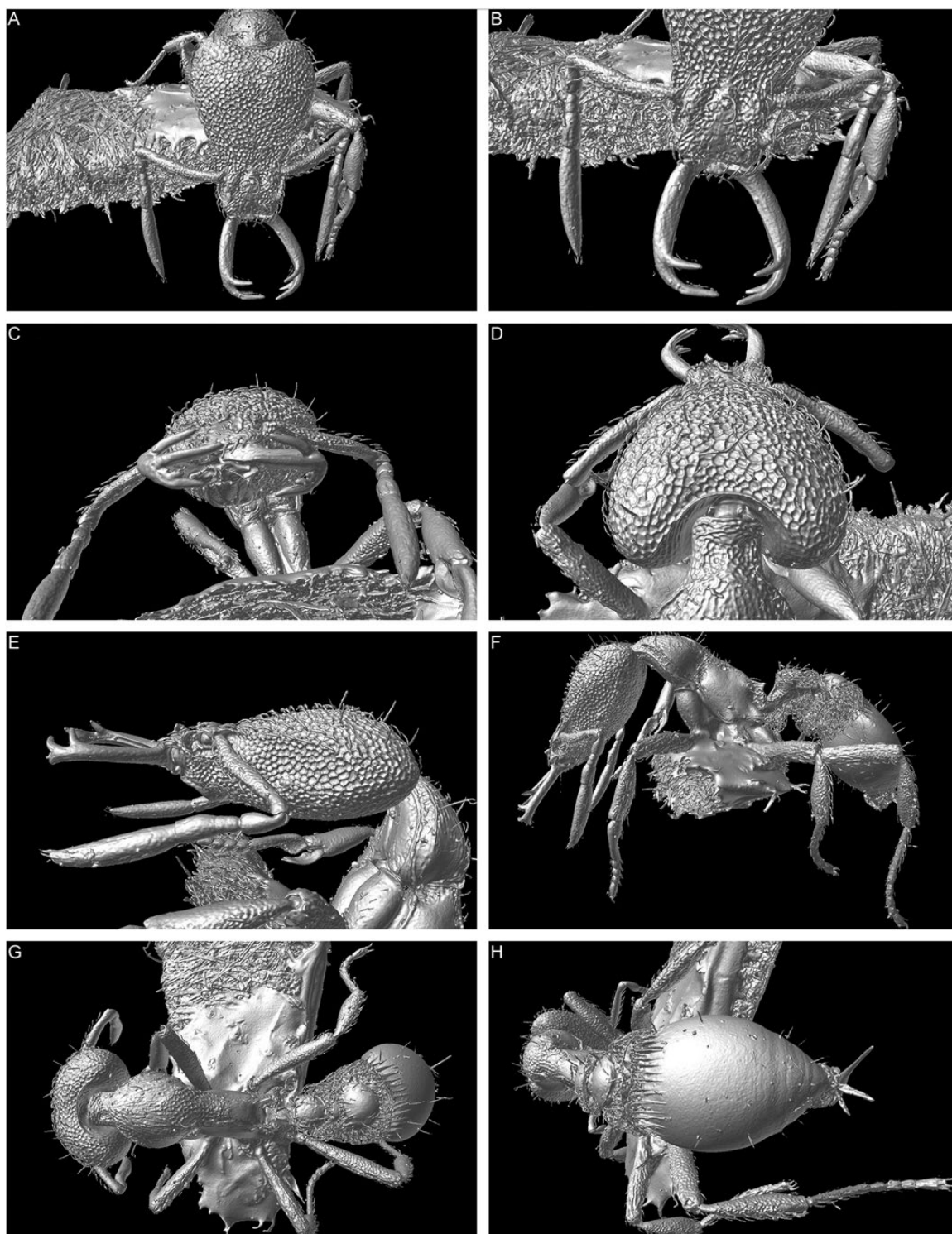
Fig. 17. Shaded surface display volume renderings of *Strumigenys frivola* (CASENT0186834). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

is so aberrant that the resemblance might be the result of convergence. Specimens collected from New Guinea and housed at the Los Angeles County Museum of Natural History were misidentified by R. Snelling as *S. basiliska* but belong instead to a putatively undescribed member of the *S. biroi* species group (D. Booher, pers. comm.). *Strumigenys basiliska* is widespread throughout the inner islands of the archipelago, though no records from Taveuni or Kadavu are known.

S. chernovi Dlussky

(Fig. 7E; Fig. 9I, J; Fig. 15, Fig. 26)

chernovi. Strumigenys chernovi Dlussky 1993: 57, figs. 2, 3; worker, queen described. Type locality: FIJI, Viti Levu, Suvy [Suva?], ii.1977 (Y. Chernov) [not examined]. Redescription of worker, in global revision (Bolton 2000: 805). In Fiji (Sarnat and Economo 2012: 128, pl. 122).
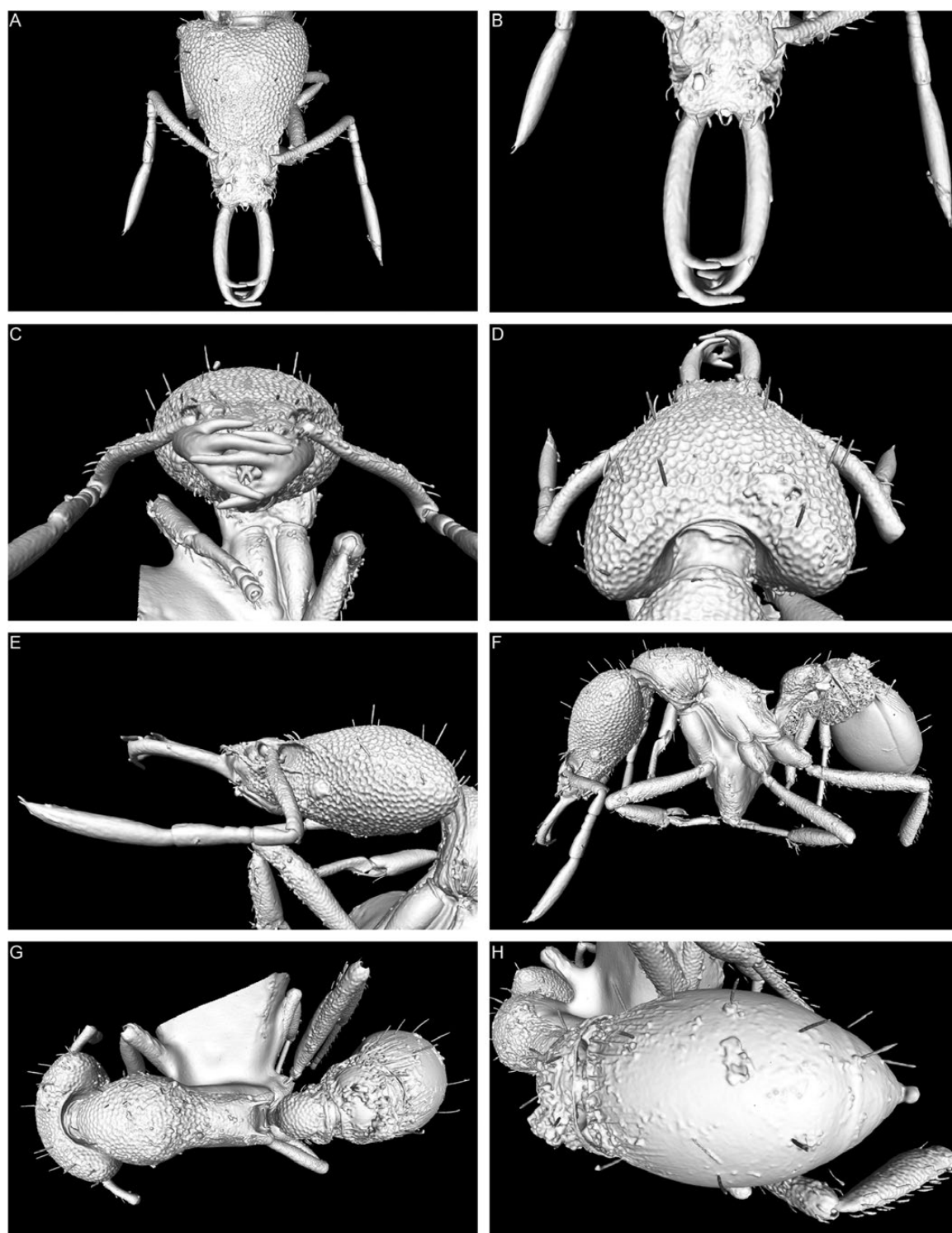
Fig. 18. [AR marker] Shaded surface display volume renderings of *Strumigenys gunter* n. sp. (CASENT0184984). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view. Scan in AR mode using Insects3D app to project 3D model.

Worker. Measurements (*n* = 10): TL 2.0-2.4, HL 0.52-0.64, HW 0.38-0.46, CI 70-74, MdL 0.22-0.28, MI 42-44, SL 0.28-0.36, SI 73-78, PW 0.23-0.28. *Strumigenys chernovi* is a long-mandible reddish brown species with filiform to flagellate hairs on the antennal scrobe margin, pronotal humeri, and hind basitarsus. The dorsal surfaces of the head, mesosoma, and waist segments are finely punctate and contrast with

the glassy smooth surface of the propodeal dorsum. The propodeal declivity is subtended by a broad convex lamella. The gastral sculpture extends approximately halfway down the first tergite.

Strumigenys chernovi belongs to a group of Fijian long-mandible endemics with filiform to flagellate hairs on the pronotal humeri and the basitarsus. This group also includes *S. daithma,*
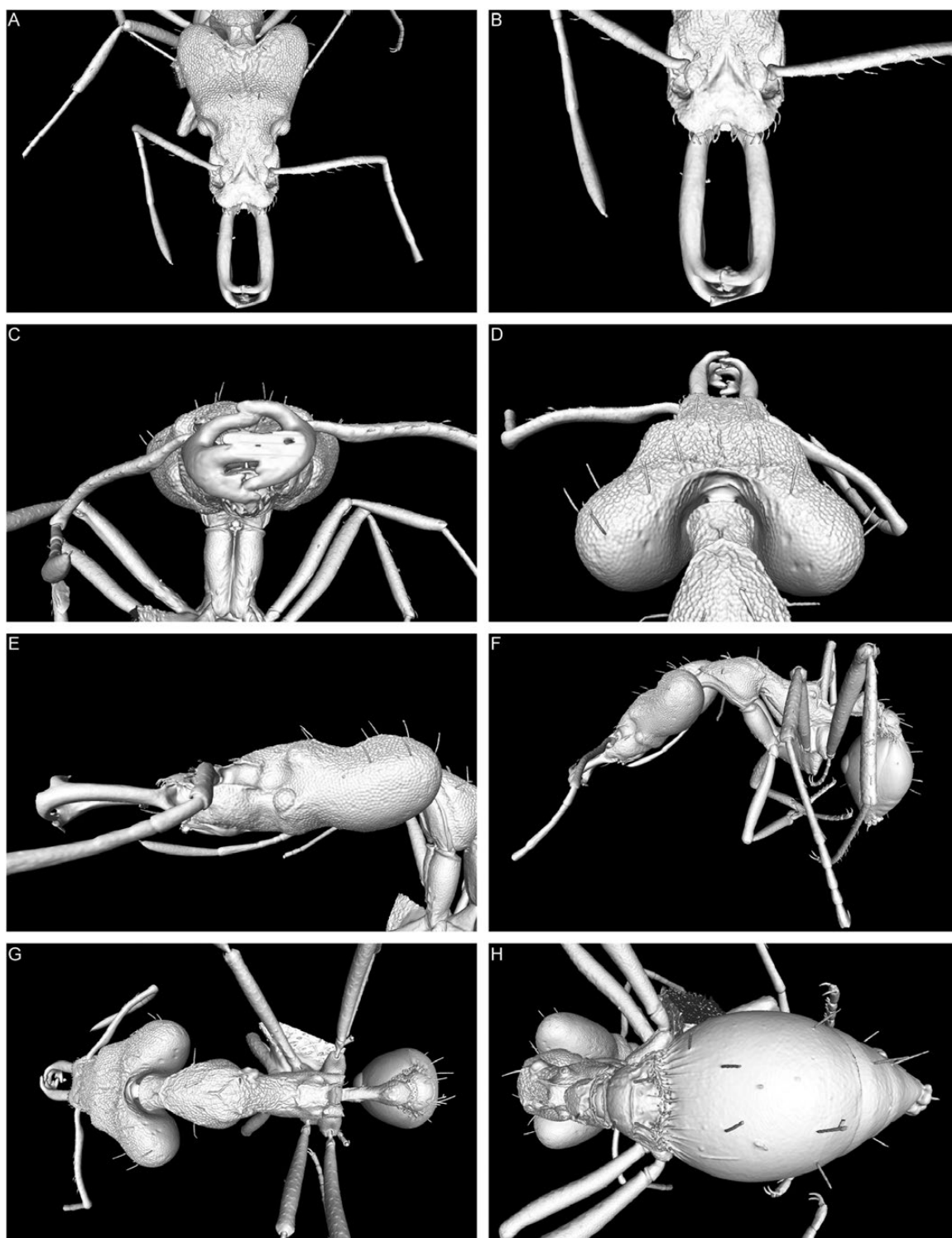
Fig. 19. Shaded surface display volume renderings of *Strumigenys mailei* (CASENT0184653). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

S. anorak, *S. ekasura*, *S. jepsoni*, *S. panaulax*, *S. scelesta*, *S. gunter*, and *S. parzival*. The tramp ant *Strumigenys godeffroyi* is superficially similar to this group, but is from an evolutionarily distinct lineage distantly related to these Fijian endemics and can be separated by the presence of sculpture on the mesopleuron. Within the group, *Strumigenys chernovi* is most similar to other species which have only one or two filiform to flagellate hairs projecting from the dorsolateral head margin; namely *S. jepsoni*, *S. panaulax*, *S. scelesta*, *S. gunter*, and *S. parzival*. Of these, *S. gunter* is the only species with a single eye facet. *Strumigenys panaulax* and *S. parzival* are the only species with gastral sculpture that extends the entire length of the first tergite. *Strumigenys chernovi* is very similar to *S. jepsoni*

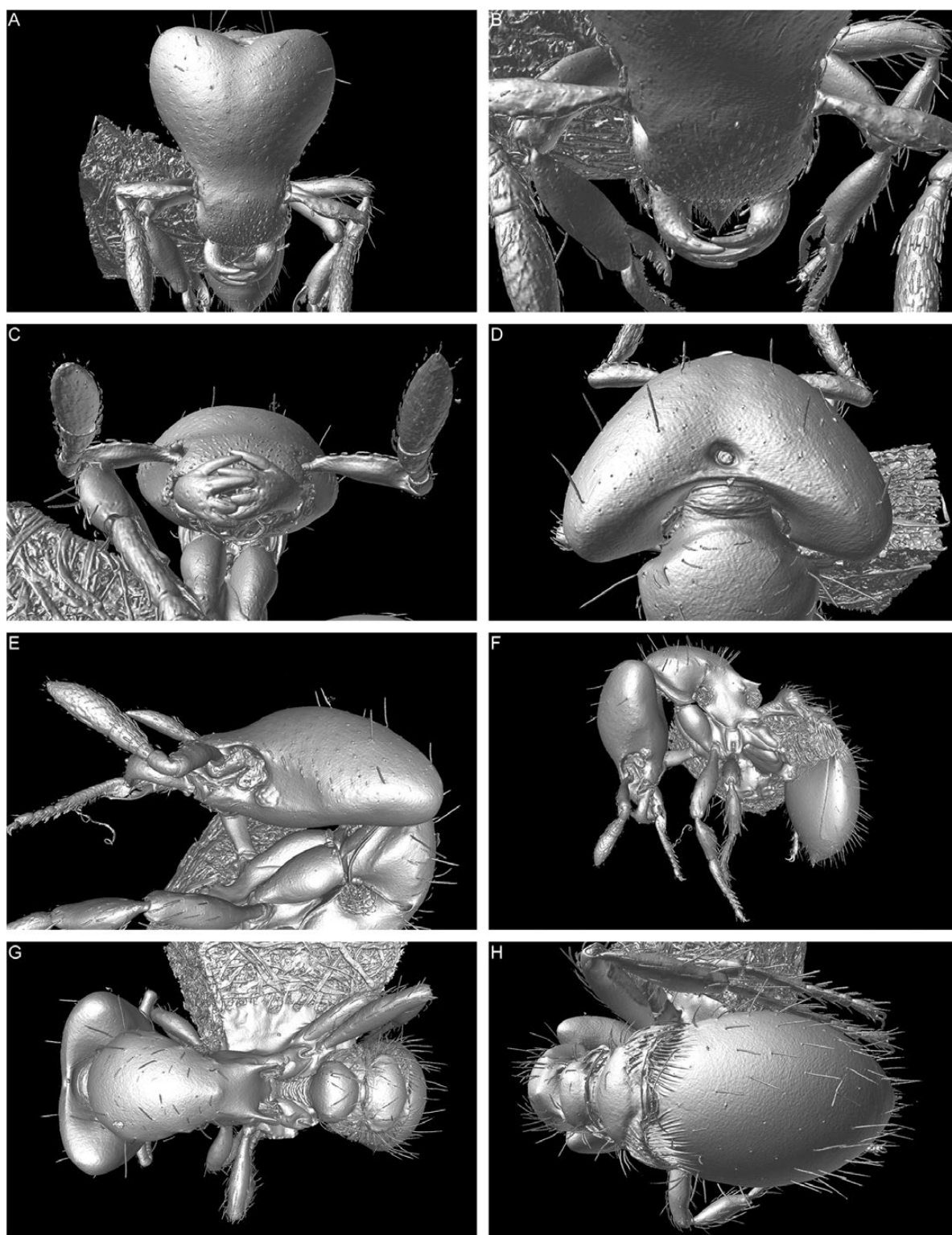**Fig. 20.** Shaded surface display volume renderings of *Strumigenys nidifex* (CASENT0185548). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

but can be separated by the dorsum of the petiole and postpetiole which is sculptured in the former but glassy smooth in the latter. Additionally, *S. chernovi* has two projecting filamentous hairs on the cephalic dorsolateral margin (one apicoscrobal and one at eye length), whereas *S. jepsoni* has only one (apicoscrobal).

Strumigenys chernovi is widespread, recorded from most of the major islands with the exceptions of Kadavu and Taveuni.

S. daithma Bolton

(Fig. 7F; Fig. 9K, L; Fig. 26)

daithma. *Strumigenys daithma* Bolton 2000: 756; worker described. Type locality: FIJI, Viti Levu, Road E of Monasavu Dam, 26.vii.1987, 17°43′S, 178°03′E, QM Berlesate No. 788, 1000 m.,

Fig. 21. [AR marker] Shaded surface display volume renderings of *Strumigenys oasis* n. sp. (CASENT0185751). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view. Scan in AR mode using Insects3D app to project 3D model.

rainforest, sieved litter, ANIC Ants vial 45.195 (G. Monteith). HOLOTYPE: worker (ANIC, not examined). In Fiji (Sarnat and Economo 2012: 128, pl. 123).

Worker. Measurements (*n* = 1): TL 2.7, HL 0.72, HW 0.52, CI 72, MdL 0.26, MI 36, SL 0.44, SI 85, PW 0.32. *Strumigenys daithma* is

a long-mandible, dark brown, coarsely sculptured species with long fine hairs covering its head and body. The apicoscrobal, pronotal humeri and basitarsal hairs are all flagellate. Although Bolton (2000) originally placed *S. daithma* in the *caniophanes*-group, results from molecular analysis suggests it belongs instead to the single radiation of Fijian endemic *Strumigenys*. Among the Fijian *Strumigenys*,
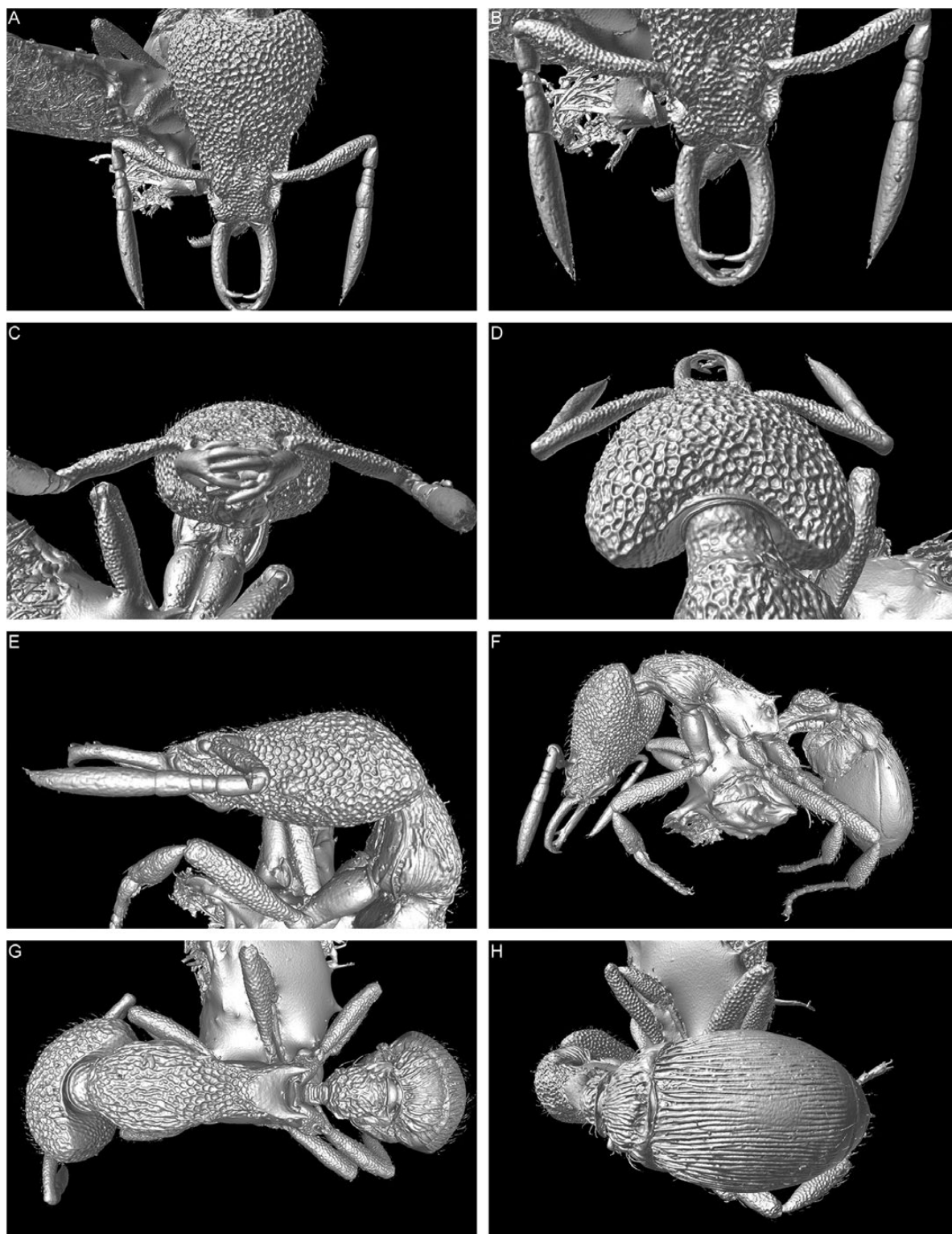
Fig. 22. [AR marker] Shaded surface display volume renderings of *Strumigenys parzival* n. sp. (CASENT0186960). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view. Scan in AR mode using Insects3D app to project 3D model.

S. daithma is most similar to *S. anorak* and *S. ekasura*, all of which have abundant filiform to flagellate hairs projecting from the dorsal surfaces of the head and mesosoma. *Strumigenys anorak* is separated from *S. daithma* and *S. ekasura* by the presence of a conspicuous, broad, convex lamella attached to the propodeal spine and declivity. *Strumigenys daithma* and *S. ekasura* are extremely similar, but Bolton (2000) separated them based on the number of projecting hairs present on the upper scrobe margin (two or more in *S. daithma*, only one in *S. ekasura*). Additionally, it appears that *S. daithma* is darker are more roughly sculptured than *S. ekasura*.
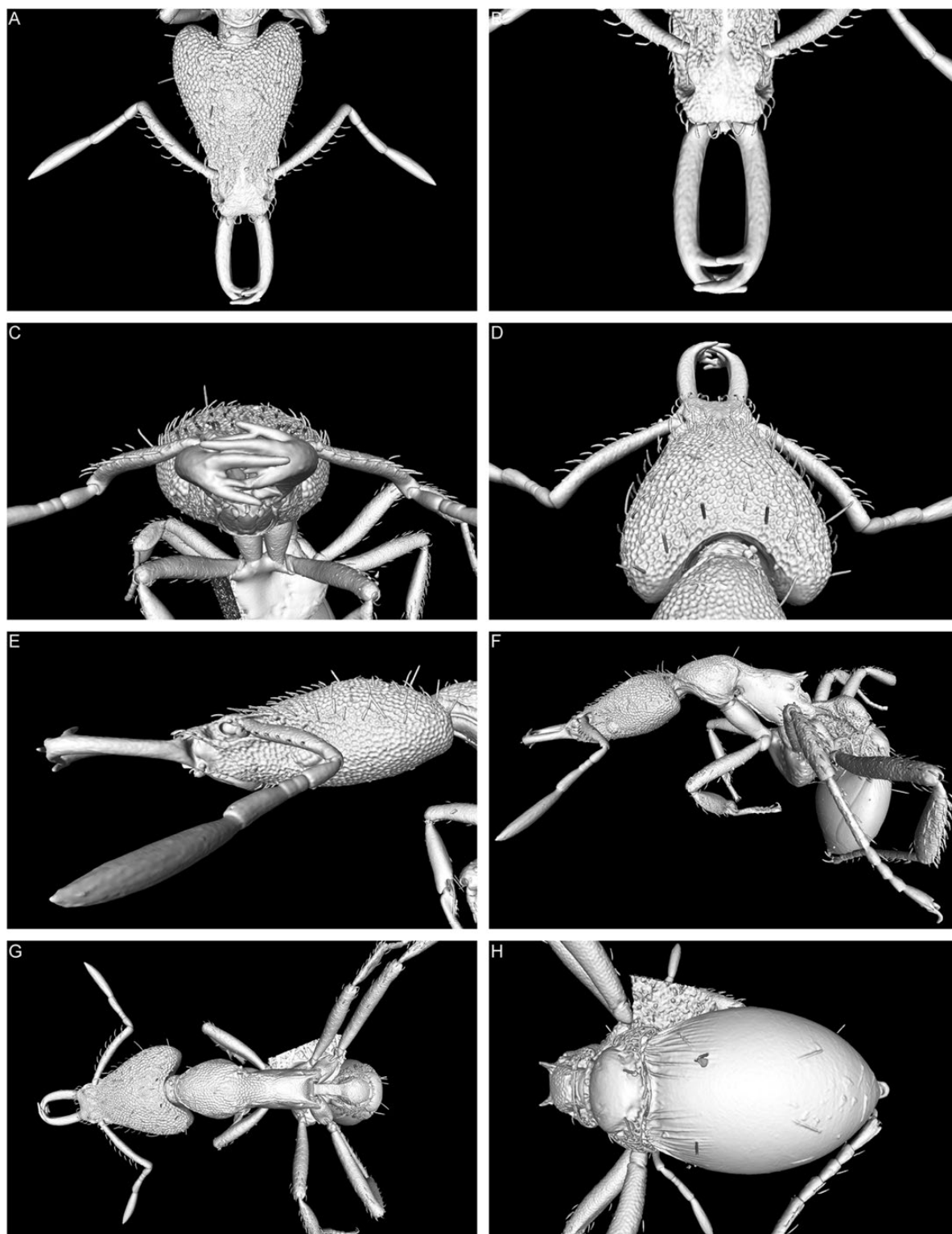
Fig. 23. Shaded surface display volume renderings of *Strumigenys praefecta* (CASENT0186943). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

The tramp ant *S. godeffroyi* is superficially similar to the aforementioned species but is distinguished by the sculptured mesopleuron and absence of filiform or flagellate hairs along the dorsolateral head margin anterior to the apicoscrobal hair.

No specimens of *S. daithma* are known besides the holotype collected near Monasavu Dam (Viti Levu).

S. ekasura Bolton

(Fig. 7G; Fig. 9M, N; Fig. 16; Fig. 26)

ekasura. *Strumigenys ekasura* Bolton 2000: 807; worker described. Type locality: FIJI, Vanua Levu, Kontiki, 19 km. E of Savusavu, 18.vii.1987, QM Berlesate No. 782, 16°48′S, 179°26′E, 20 m., secondary
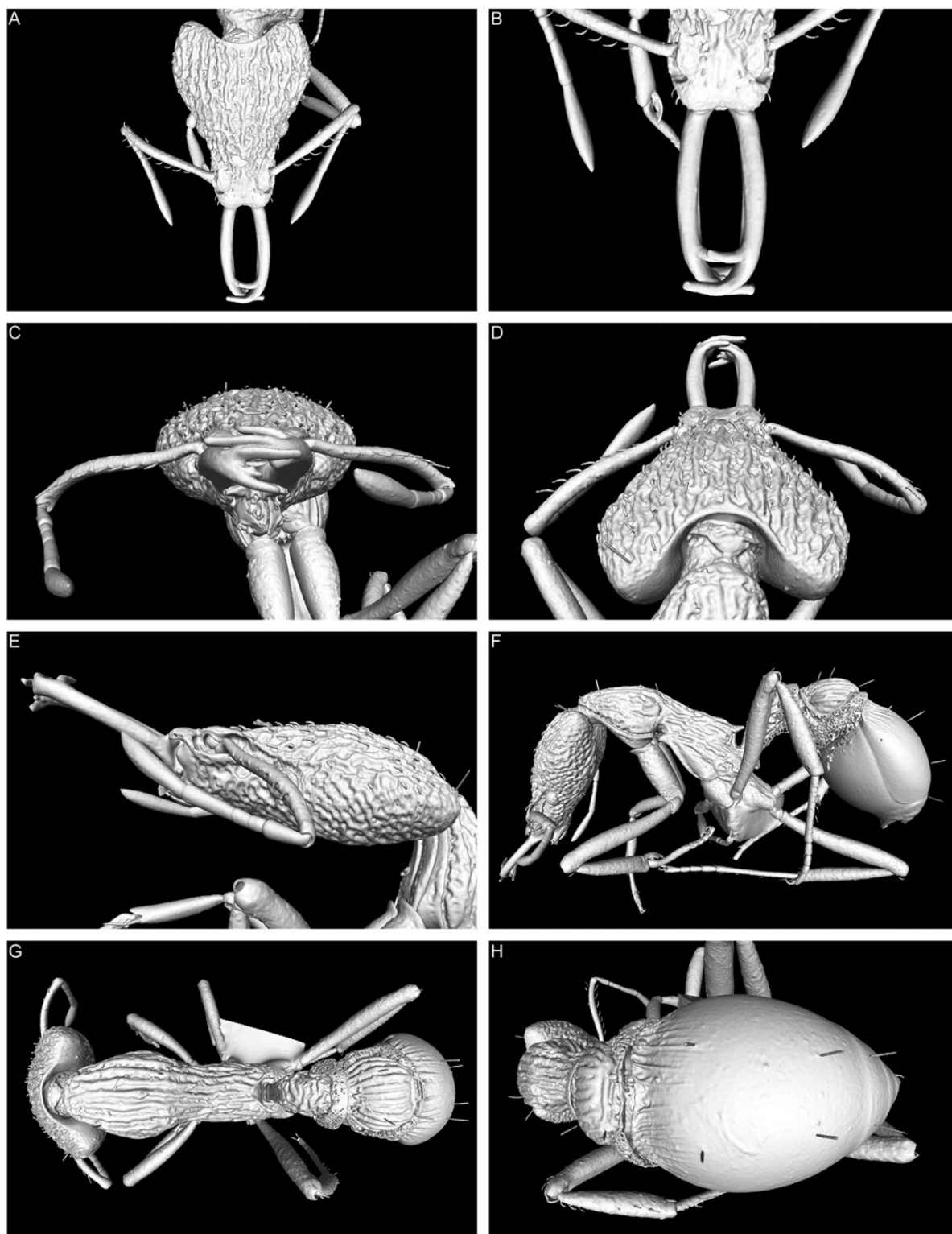
Fig. 24. Shaded surface display volume renderings of *Strumigenys sulcata* (CASENT0185705). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

rainforest, sieved litter (G. Monteith). HOLOTYPE: worker (ANIC, not examined). In Fiji (Sarnat and Economo 2012: 129, pl. 124).

Worker. Measurement (n = 1): TL 2.3, HL 0.60, HW 0.42, CI 70, MdL 0.22, MI 37, SL 0.35, SI 83, PW 0.27. *Strumigenys ekasura*

is long-mandible species characterized by abundant free-stranding flagellate pilosity on all dorsal surfaces, a sculptured postpetiolar disc, conspicuous basigastral pilosity, and the lack of a propodeal lamella. The species was originally ascribed by Bolton (2000) to the *smythiesii*-species group, but belongs instead to the single in
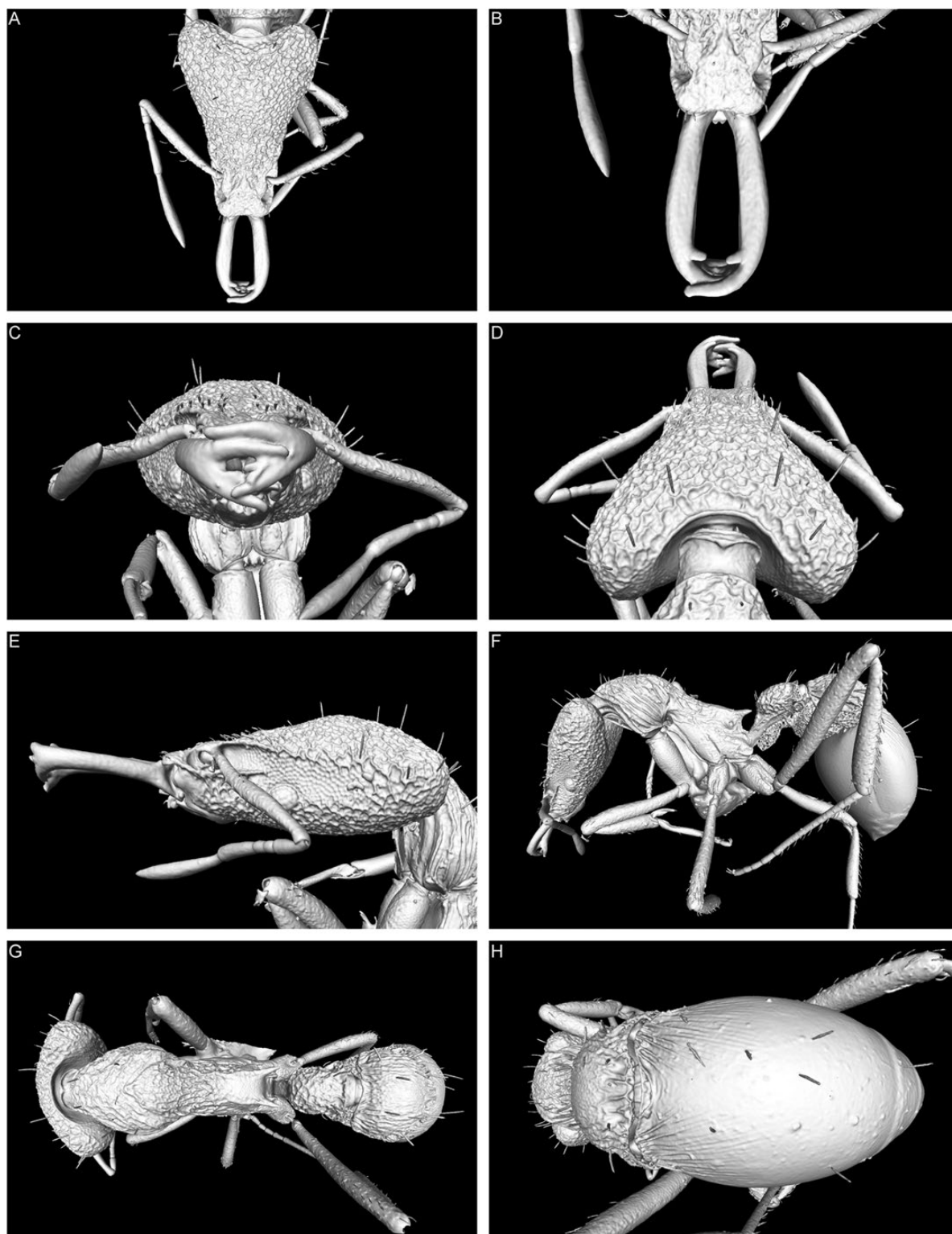
Fig. 25. Shaded surface display volume renderings of *Strumigenys tumida* (CASENT0185699). (A) Full-face view, (B) mandibles in full face view, (C) mandibular apical fork, (D) head in posterodorsal view, (E) head in profile view, (F) profile view, (G) dorsal view, (H) gaster in dorsal view.

situ radiation of Fijian *Strumigenys* (Booher and Economo, unpublished data). *Strumigenys ekasura* is most similar in appearance to several other Fijian species with abundant filiform and flagellate hairs on the head and mesosoma—namely *S. anorak*, *S. daithma*, and to a lesser extent *S. chernovi*. In addition to the characters given in the key, we refer readers to the notes given under the latter two species accounts for discussion on how to separate *S. ekasura* from similar Fijian *Strumigenys*. The species is widespread and is recorded from most of the major islands with the exception of Taveuni and Ovalau.
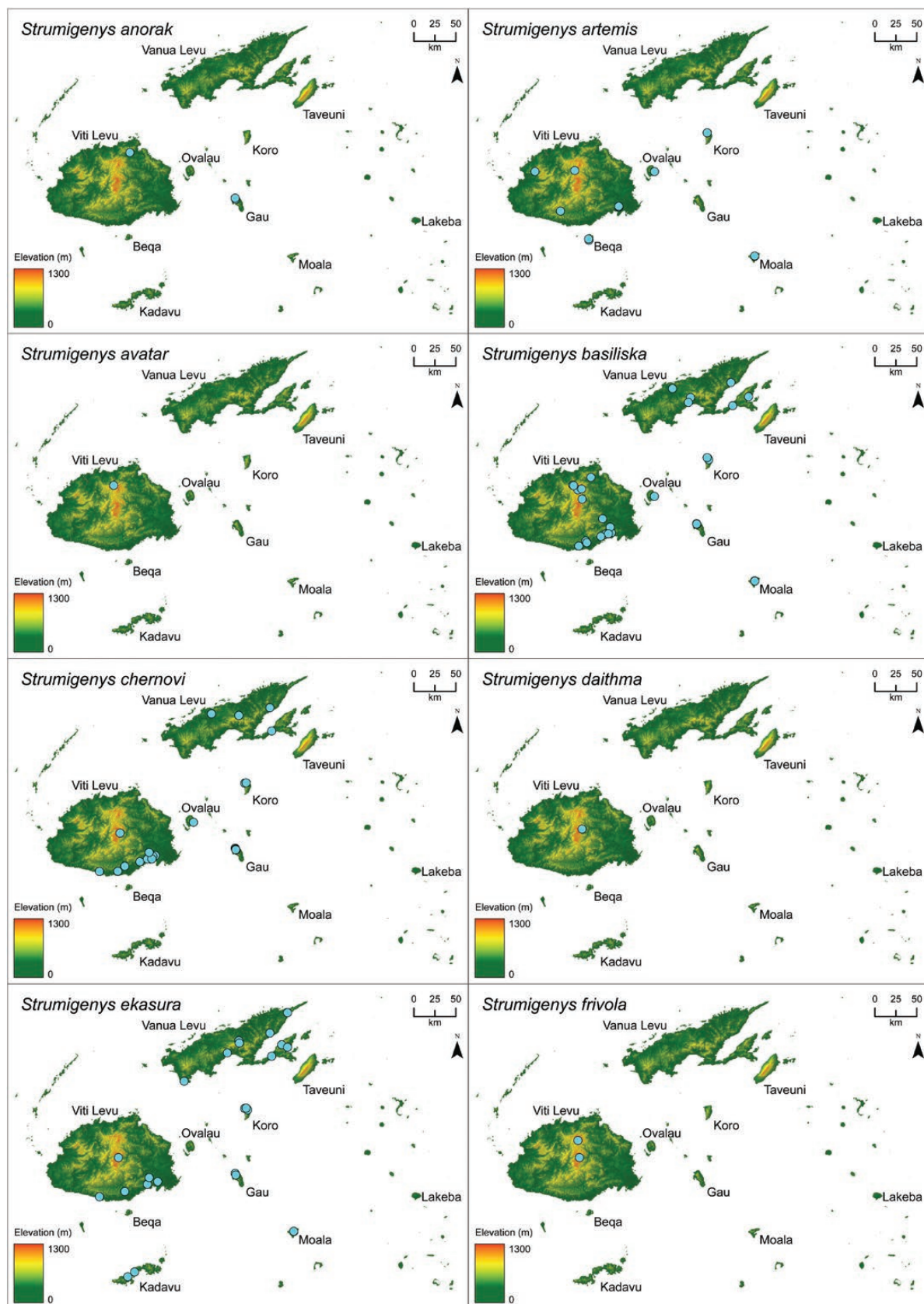
Fig. 26. Distribution maps of *Strumigenys* species on the Fiji Islands. The following species are presented: *S. anorak*, *S. avatar*, *S. artemis*, *S. basiliska*, *S. chernovi*, *S. daithma*, *S. ekasura*, *S. frivola*.
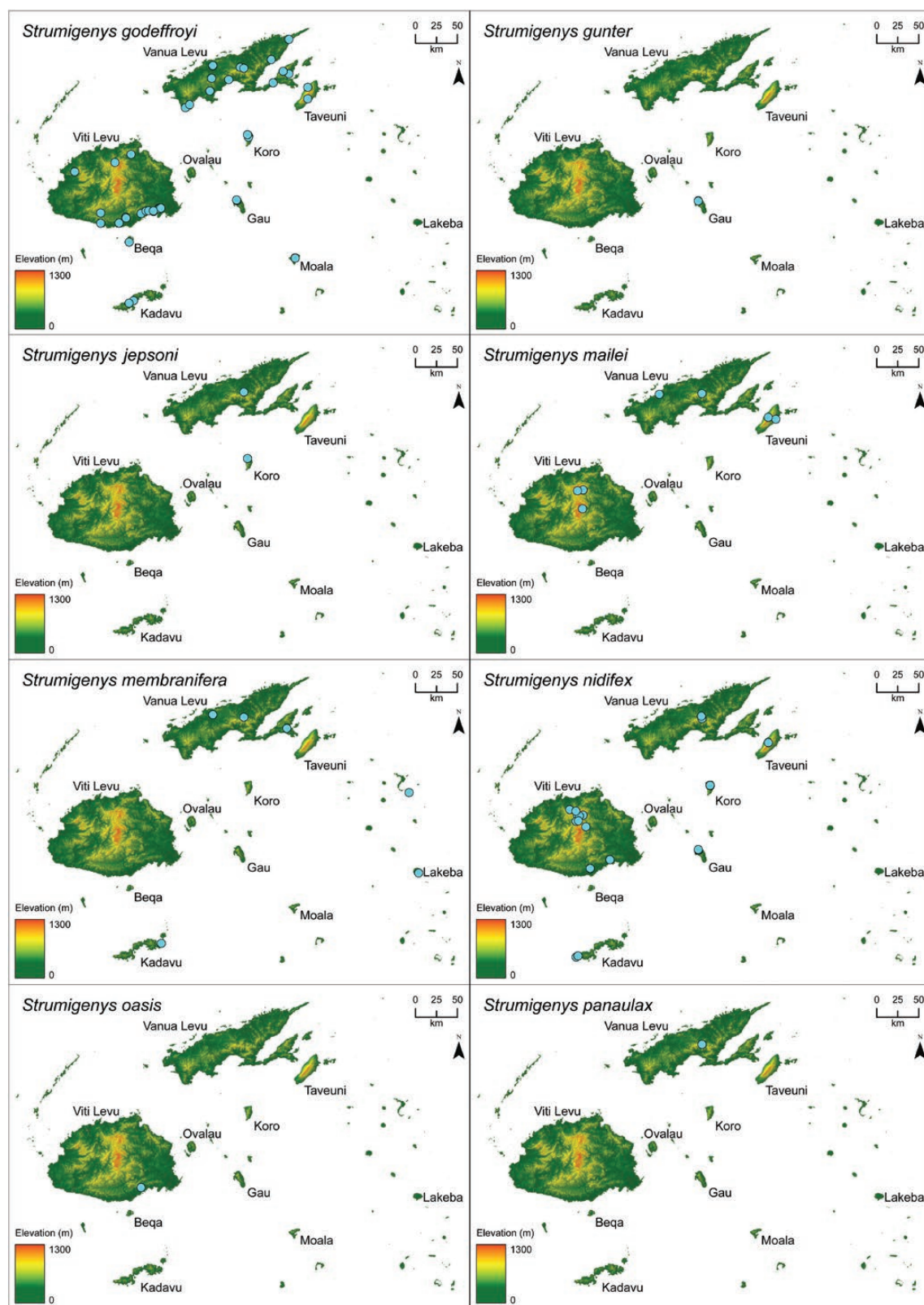
Fig. 27. Distribution maps of *Strumigenys* species on the Fiji Islands. The following species are presented: *S. godeffroyi, S. gunter, S. jepsoni, S. mailei, S. membranifera, S. nidifex, S. oasis, S. panaulax.*

S. frivola Bolton

(Fig. 7H; Fig. 9O, P; Fig. 17; Fig. 26)

frivola. Strumigenys frivola Bolton 2000: 817; worker described.
  Type locality: FIJI, Viti Levu, Nadarivatu Reserve, 850 m.,

11.vii.1987, pyrethrum/trees and logs (G. & S. Monteith). HOLOTYPE: worker (ANIC, examined). PARATYPE: worker (BMNH, examined). In Fiji (Sarnat and Economo 2012: 129, pl. 125).

Worker. Measurements (n = 2): TL 2.5, HL 0.60–0.62, HW 0.43–0.44, CI 69–73, MdL 0.25–0.26, MI 42, SL 0.37, SI 84–86, PW 0.29. *Strumigenys frivola* is an opaque yellow brown species with long mandibles, punctate sculpture, and short recumbent pilosity covering its head, most of the mesosoma, and both waist segments. The apicoscrobal and pronotal humeral hairs are short and flagellate. The basigastral costulae are conspicuous and long, and the propodeum lacks lamellae. Bolton originally placed
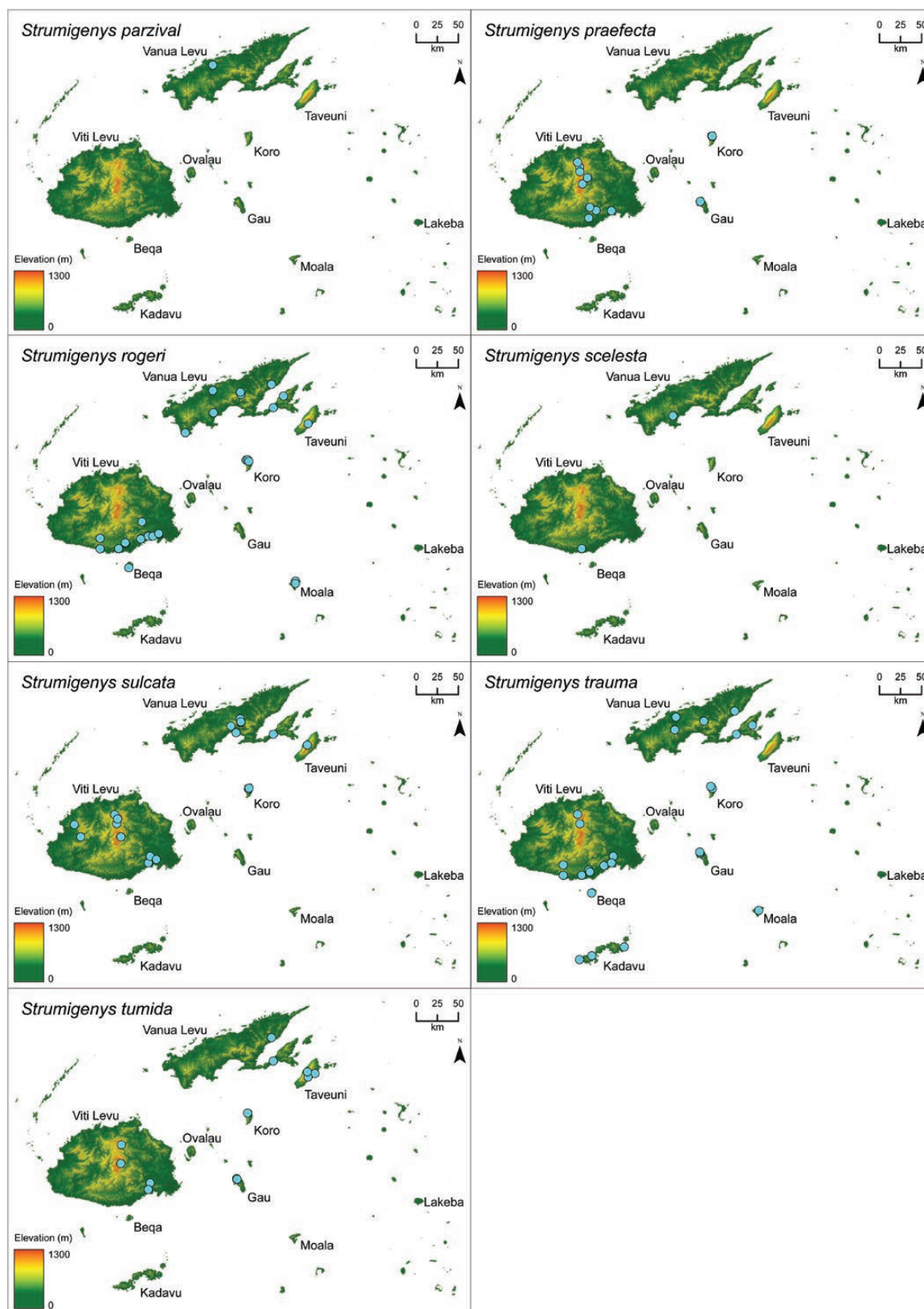

Fig. 28. Distribution maps of *Strumigenys* species on the Fiji Islands. The following species are presented: *S. parzival, S. praefecta, S. rogeri, S. scelesta, S. sulcata, S. trauma, S. tumida.*
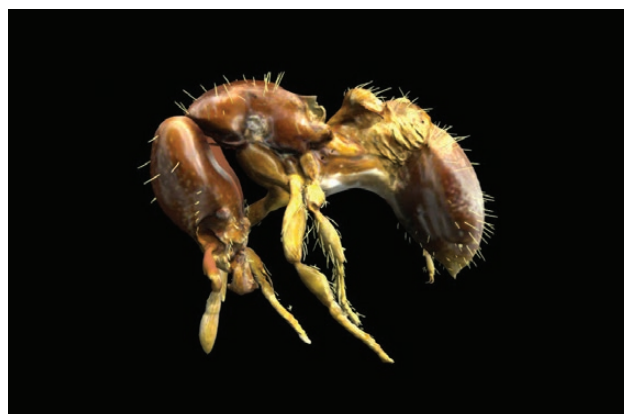
Model 1. *Strumigenys anorak* (CASENT0186900, holotype) presented as a computer generated 3D mesh model optimized for augmented reality. Volumetric surfaces rendered from micro-ct data and texture mapped from standard specimen photographs. An interactive version of this model is available in the HTML version of this article online and at https://sketchfab.com/3d-models/9bdd4f1426a44a27996289172a2bbe33

Model 2. *Strumigenys artemis* (CASENT0186982) presented as a computer generated 3D mesh model optimized for augmented reality. Volumetric surfaces rendered from micro-ct data and texture mapped from standard specimen photographs. An interactive version of this model is available in the HTML version of this article online and at https://sketchfab.com/3d-models/616f07097a7e4b4ca5ae38e6d14ff6c5

Model 3. *Strumigenys avatar* (CASENT0185902, holotype) presented as a computer-generated 3D mesh model optimized for augmented reality. Volumetric surfaces rendered from micro-ct data and texture mapped from standard specimen photographs. An interactive version of this model is available in the HTML version of this article online and at https://sketchfab.com/3d-models/b258462cc47c44d48e5b9edf8b50e632

Model 4. *Strumigenys gunter* (CASENT0184984, holotype) presented as a computer-generated 3D mesh model optimized for augmented reality. Volumetric surfaces rendered from micro-ct data and texture mapped from standard specimen photographs. An interactive version of this model is available in the HTML version of this article online and at https://sketchfab.com/3d-models/2e5ace8bb36843b19a41b0c9f7f2b842

Model 5. *Strumigenys oasis* (CASENT0185751, holotype) presented as a computer-generated 3D mesh model optimized for augmented reality. Volumetric surfaces rendered from micro-ct data and texture mapped from standard specimen photographs. An interactive version of this model is available in the HTML version of this article online and at https://sketchfab.com/3d-models/002454768d2a4409b922b09222fc80a1

Model 6. *Strumigenys parzival* (CASENT0186960, holotype) presented as a computer-generated 3D mesh model optimized for augmented reality. Volumetric surfaces rendered from micro-ct data and texture mapped from standard specimen photographs. An interactive version of this model is available in the HTML version of this article online and at https://sketchfab.com/3d-models/2d608f095a1d4daea3ba34e0cae83255

S. frivola in the *rofocala* complex as a matter of convenience because it lacks erect flagellate hairs on the dorsal surface of the hind basitarsus, but suggested (correctly) that it might be more closely related to other Fijian endemics. *Strumigenys artemis* and *S. mailei* are similar in appearance to *S. frivola* and also lack flagellate basitarsal hairs. Whereas the apicoscrobal and humeral hairs of *S. frivola* are flagellate, those of the other two species are simple. Furthermore, the only erect hairs on the pronotal dorsum of *S. frivola* are the humeral hairs, whereas the other two species have pairs of erect hairs on their pronotal dorsa in addition to the humeral pair.

    Strumigenys frivola is apparently quite rare, as it is known only from the type locality at Nadarivatu (Viti Levu), a nest collection from nearby Mt. Tomanivi, and a fogging sample at the nearby Monasavu Dam area.

S. godeffroyi Mayr

(Fig. 7I; Fig. 9Q, R; Fig. 27)

godeffroyi. Strumigenys godeffroyi Mayr 1866[88]: 516; worker described. Type locality: SAMOA [not examined]. Queen described (Mayr 1887: 569). Karyotyped (Imai *et al.* 1984: 68). In global revision (Bolton 2000: 791). In Fiji (Sarnat and Economo 2012: 130, pl. 126).

indica. Strumigenys Godefroyi var. indica Forel 1902: 243 (q.) INDIA, Thana [Thane]. Junior synonym of *godeffroyi*: Brown 1949: 17.

butteli. Strumigenys godeffroyi var. butteli Forel 1913: 83 (w.q.). SRI LANKA, Peradeniya. Junior synonym of *godeffroyi*: Brown 1949: 17.

geococci. Strumigenys godeffroyi subsp. *geococci* Calilung 2000: 70, Fig. 3 (w.) PHILIPPINES Luzon, Laguna, Mt. Makiling, on roots of Beaucarnea recurvata (Lem.) Hemsl., 23 iv. 1988 (MV. J. Calilung, MVJC099) (UPLB-MNH). Junior synonym of *godeffroyi*: Bolton 2000: 791.

Worker. Measurements (*n* = 20): TL 2.1–2.5, HL 0.54–0.64, HW 0.40–0.45, CI 67–73, MdL 0.24–0.30, MI 45–49, SL 0.33–0.40, SI 86–95, PW 0.26–0.28. *Strumigenys godeffroyi* is a reddish brown, long-mandible, strongly pilose species with many pairs of long flagellate hairs on the mesosoma and metasoma in addition to a dense ground pilosity consisting of semidecumbent hairs on the cephalic and mesosomal dorsal surfaces. The apicoscrobal, humeral, and basitarsal hairs are all long a flagellate. The propodeal lamella is extensive and covers the propodeal spine. *Strumigenys godeffroyi* is superficially similar to other Fijian *Strumigenys* species with extensive filiform and flagellate pilosity, namely *S. daithma, S. anorak*, and *S. ekasura*. Whereas the mesopleuron of *S. godeffroyi* is reticulate-punctate, that of the aforementioned species is polished smooth. Moreover, the other species all have multiple pairs of filiform to flagellate hairs projecting from the dorsolateral cephalic margin between the apicoscrobal hair and the eye, while *S. godeffroyi* has only the projecting apicoscrobal hairs. The propodeal lamella is strongly produced in *S. godeffroyi*, appearing quite thick in dorsal view. *Strumigenys daithma* and *S. ekasura* lack propodeal lamellae entirely, and those of *S. anorak* are much thinner with the propodeal spines clearly visible. Although likely native to Southeastern Asia, *Strumigenys godeffroyi* did not descend from the ancestor of the Fijian *Strumigenys* radiation. It is a successful tramp species that has spread across the Pacific and has been recorded from most of Fiji's major islands.

S. gunter n. sp.

(Fig. 7J; Fig. 9S, T; Fig. 18; Fig. 27, Model 4)

(Zoobank LSID: urn:lsid:zoobank.org:act:F8D09061-DA1C-454E-91B2-634905A1CA02)

HOLOTYPE. Fiji, Gau I., Mt. Delaco, 2.8 km SE Navukailagi Village, 2008-02-07, 432m, –17.9795° 179.2760°, primary rainforest, sifted litter, E.P. Economo, EPE291.16 (worker, dry pinned, BPBM, specimen code CASENT0184984).
= *Strumigenys* sp. FJ14 (Sarnat and Economo 2012: 136, pl. 138)

Cybertype. Volumetric raw data (in DICOM format) of the physical holotype (CASENT0184984) is deposited at Dryad (https://doi.org/10.5061/dryad.1f9d55b/4) and can be freely accessed as virtual representation of the type. In addition to the cybertype data at Dryad, we also provide a freely accessible 3D surface model of the holotype at Sketchfab (https://skfb.ly/6vsHN).

    Worker. Measurements (*n* = 2): TL 2.41–2.44 mm, HL 0.55–0.58 mm, HW 0.39–0.43 mm, CI 70–74, MdL 0.23–0.27 mm, MI 42–47, SL 0.37–0.41 mm, SI 81, PW 0.24–0.26 mm, PI 59–61, FL 0.37–0.41 mm, FI 94–96, EL 0.24–0.26 mm. Color a pale yellowish-brown. Mandibles long and linear with one preapical tooth; preapical tooth length approximate to maximum mandible width. Apicoscrobal hair short and simple, weakly projecting laterally but not filiform or flagellate. Cephalic dorsum uniformly reticulate-punctate. Ground pilosity of cephalic dorsum short, simple, strongly curved. Pronotal humeral hairs thin, flexuous, of moderate length. Promesonotal dorsum with short curved ground pilosity and two pairs of longer erect hairs in addition to humeral pair. Pronotal dorsum with weak longitudinal striae. Mesonotal dorsum weakly reticulate-punctate. Propodeal dorsum smooth and shining. Pronotal sides weakly striate apically; remainder of mesosomal sides smooth and shining. Propodeal tooth short, narrowly triangular, embedded in lamella. Lamella forming convex curtain along propodeal declivity. Femur and tibia of hind leg both with single filiform projecting hair on dorsal surface. Petiolar node in profile with anterior face slightly steeper and shorter than posterior face; lateral spongiform lobe small; restricted to posterior margin of node. Dorsum of petiole and petiolar disc smooth and shining; each with two pairs of filiform to flagellate hairs. Ventral lobe of postpetiole spongiform. First gastral tergite with erect filiform hairs. Basigastral sculpturing consists of broadly spaced costulae shorter in length than postpetiolar disc.

    Strumigenys gunter is a small shiny pale-yellow species with small eyes of one to several facets, abundant long flexous hairs on metasomal dorsum, and shorter subdecumbent hairs on the promesonotum. It morphologically similar to a cluster of species related to *S. chernovi*, but is immediately distinguished by the smaller eyes. Additional diagnostic notes are given under *S. chernovi*. *Strumigenys gunter* is only known from three worker specimens collected on Gau and Koro.

    Etymology: *Gunter* is a contraction of 'egg' and 'hunter' in the fictional work *Ready Player One* (Cline 2011) and refers to particular users of the virtual reality world OASI*S*. The name is a noun in apposition and thus invariable.

S. jepsoni Mann

(Fig. 7K; Fig. 9U, V; Fig. 27)

jepsoni. Strumigenys jepsoni Mann 1921: 462, Fig. 22a; worker described. Type locality: FIJI, Vanua Levu, Suene (W. M. Mann).

Syntypes: 2 workers (MCZC type no. 21099, examined); 4 workers (USNM, examined). In global revision (Bolton 2000: 809). In Fiji (Sarnat and Economo 2012: 130, pl. 127).

Worker. Measurements (*n* = 7): TL 2.4–2.7, HL 0.59–0.66, HW 0.43–0.48, CI 72–73, MdL 0.24–0.28, MI 41–42, SL 0.34–0.40, SI 77–83, PW 0.26–0.30. *Strumigenys jepsoni* is a small, long-mandible, reddish-brown species with short pilosity and strongly shining dorsal surfaces of the petiole and postpetiole. The apicoscrobal and pronotal humeral hairs are relative short and stiff, the basitarsal hair is flagellate, and the propodeal lamella are broad and conspicuous in profile. *Strumigenys* is most similar to *S. gunter* and *S. scelesta*, as all three species have flagellate basitarsal hairs, and no laterally projecting hairs on the cephalic dorsum save the apicoscrobal pair. Whereas *S. jepsoni* and *S. gunter* have at least one pair of erect hairs on the pronotal dorsum in addition to the humeral hairs, *S. scelesta* has none. *Strumigenys jepsoni* is most reliably separated from *S. gunter* by its larger eye.

Strumigenys jepsoni was named after Mr. F. P. Jepson, Entomologist of Fiji. The species was not collected during the major 2002–2008 surveys of Fijian ants (Sarnat and Economo 2012). The only two records of the species are both from Vanua Levu.

S. mailei Wilson & Taylor

(Fig. 7L; Fig. 9W, X; Fig. 19; Fig. 27)

mailei. *Strumigenys mailei* Wilson & Taylor 1967: 38, Fig. 28; worker described. Type locality: SAMOA, Afiamalu, 800 m., 15.iii.1962, rain forest, berlesate of moss on tree, 10–13 m. from ground, no. 581 (R. W. Taylor). HOLOTYPE: 1 worker (MCZC type no. 31114, examined). PARATYPE: 1 worker (MCZC type no. 31114, examined) [PARATYPE locality: FIJI, Viti Levu, Navai Mill, nr. Nadarivatu, 800 m., 17.ix.1938 (E. C. Zimmerman)]. In global revision (Bolton 2000: 823). In Fiji (Sarnat and Economo 2012: 130, pl. 128).

Worker. Measurements (*n* = 7): TL 2.4–2.9, HL 0.62–0.74, HW 0.43–0.50, CI 66–70, MdL 0.29–0.34, MI 46–50, SL 0.38–0.45, SI 88–92, PW 0.28–0.31. Originally described from Samoa, *Strumigenys mailei* is a reddish-brown long-mandible species with short and stiff apicoscrobal and pronotal humeral hairs, no flagellate basitarsal hairs, and no conspicuous propodeal lamella. It also has many pairs of short, straight, erect hairs on the dorsal surfaces of the head, mesosoma, and metasoma. Of the Fijian *Strumigenys* that lack flagellate basitarsal hairs but possess pronotal humeral hairs, *S. mailei* is most similar to *S. frivola* and *S. artemis*. Whereas the humeral hairs of *S. frivola* are flagellate, those of the *S. mailei* and *S. artemis* are stiff and simple. These latter two are most reliably separated from *S. artemis* by the ground pilosity of the head and mesosoma, which is short and subdecumbent in *S. artemis* versus finer and erect in *S. mailei*. In Fiji, *Strumigenys mailei* is known from Viti Levu, Vanua Levu, and Taveuni. The name is based on the Samoan word for 'trap' and alludes to the remarkable, trap-like action of the mandibles of *Strumigenys* workers (Wilson and Taylor 1967).

S. membranifera Emery

(Fig. 8A; Fig. 10A, B; Fig. 27)

membranifera. *Strumigenys* (*Trichoscapa*) *membranifera* Emery 1869: 24, Fig. 11; worker described. Type locality: ITALY [not

examined]. Combination in *Strumigenys* (*Cephaloxys*): Emery 1916: 205; in *Trichoscapa*: Brown 1948: 113; in *Pyramica*: Bolton 1999: 1673; in *Strumigenys*: Baroni Urbani & De Andrade 2007: 123. In Fiji (Mann 1921: 461, Fig. 22c; Sarnat and Economo 2012: 118, pl. 114); in Polynesia (Wilson & Taylor 1967: 35, Fig. 24). In generic revision (Bolton 2000: 322).

simillima. *Strumigenys* (*Trichoscapa*) *membranifera* r. *simillima* Emery 1890: 69, pl. 8, Fig. 5 (w.) ANTILLES. Combination in *Strumigenys* (*Cephaloxys*): Emery 1924: 325. Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

santschii. *Strumigenys* (*Trichoscapa*) *membranifera* var. *santschii* Forel 1904: 6 (w.) TUNISIA, Kairouan. Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

silvestriana. *Strumigenys silvestriana* Wheeler 1928: 27 (w.) CHINA, Macao. Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

foochowensis. *Strumigenys* (*Cephaloxys*) *foochowensis* Wheeler 1928: 28 (q.) CHINA, Foochow. Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

marioni. *Strumigenys* (*Trichoscapa*) *membranifera* var. *marioni* Wheeler 1933: 276 (w.) U.S.A., Mississippi. Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

williamsi. *Strumigenys* (*Trichoscapa*) *membranifera* var. *williamsi* Wheeler 1933: 276 (w.q.) U.S.A., Hawaii, off the road to Puna, south of Olaa, Hawaii, under moss, etc., iv.1932 (*F.X. Williams*). Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

vitiensis. *Strumigenys* (*Cephaloxys*) *vitiensis* Mann 1921: 461, Fig. 22 (w.) FIJI, Vanua Levu, Lasema. Junior synonym of *Strumigenys membranifera*: Brown 1948: 114.

Worker. Measurements (n = 10). TL 1.9–2.1, HL 0.46–0.50, HW 0.40–0.44, CI 84–90, MdL 0.08–0.10, MI 16–20, SL 0.22–0.24, SI 51–57, PW 0.23–0.26. *Strumigenys membranifera* is a short mandible species with a strongly convex cephalic dorsum that bears a single pair of standing hairs. It can be separated from Fiji's native short mandible species, *S. trauma*, by the lack of pronotal humeral hairs and the smooth dorsal surfaces of its mesosoma and petiole. Wilson and Taylor (1967) offered the following discussion of *S. membranifera*, 'Brown (1949) states that *T. membranifera* [= *S. membranifera*] is probably of African origin. It has been spread by human commerce through a large part of the tropics and warm temperate zones, including such diverse areas as the Fiji Is., eastern China, West Indies and southeastern United States. The species has an ecological amplitude unusual for a dacetine, nesting in major habitats from dense woodland to dry, open cultivated fields'. Wilson (1954) described the feeding behavior of the workers as being predaceous on a wide variety of small, soft-bodied arthropods. In Fiji, the species is relatively rare, and during the recent surveys (Sarnat and Economo 2012) was represented by a single collection of specimens from a litter sample taken at Rokosalase (Vanua Levu). Several older collections from Fiji were also recorded from museums.

S. nidifex Mann

(Fig. 8B; Fig. 10C, D; Fig. 20; Fig. 27)

nidifex. *Strumigenys nidifex* Mann 1921: 464, Fig. 23; worker, queen, male described. Type locality: FIJI, Viti Levu, Nadarivatu (W. M. Mann). Syntypes: 7 workers, 2 queens (MCZC type no. 8710, examined); 1 worker, 4 queens, 1 male (USNM, examined). Larva described (Wheeler and Wheeler 1955: 140). Discussed (Brown

1954). In revision of *szalayi* group (Brown 1971: 81); in global revision (Bolton 2000: 905). In Fiji (Sarnat and Economo 2012: 131; pl. 129).

Note: Specimens from the nontype locality of Buka Levu (USNM), Waiyanitu (MCZC), and Veisari (MCZC) bear red cotype labels but are not true syntypes (Sarnat and Economo 2012: 131).

Worker. Measurements (n = 10): TL 4.7–5.1, HL 1.38–1.48, HW 0.98–1.13, CI 71–76, MdL 0.62–0.64, MI 43–46, SL 0.88–0.94, SI 83–90, PW 0.46–0.51. *Strumigenys nidifex* is one of the most conspicuous *Strumigenys* of the Fijian fauna, and among the largest *Strumigenys* on the planet. The species has a distinctively broad head that is impressed posterior to the vertex and bears a preocular impression on the ventrolateral margin of the head. All surfaces of the head, mesosoma, waist, and coxae are reticulate-punctate. The nearest relative to *S. nidifex* is *Strumigenys avatar*. The gaster of the former is sculptured basally, but is otherwise strongly polished and shiny. The gaster of the latter is strongly punctate-striate the entire length of the first segment. The males of the two differ, with those of *S. nidifex* being larger with a distinctly elongated head, while the male of *Strumigenys avatar* is smaller with a much rounder head. The queen of *Strumigenys avatar* is also distinctly smaller, especially with regard to the mesonotum. However, the series of *S. nidifex* from Koro are all smaller, and the queens of that series are more similar to those of *Strumigenys avatar* than to those of its conspecifics on other islands, with the caveat that its gaster is polished and shiny. Both species occur sympatrically in the Nadarivatu area. The only other species in Fiji with a preocular notch is *S. rogeri*, which is easily separated by its significantly smaller size, yellow brown color, and mandible with two preapical teeth. The other large *Strumigenys* in Fiji all lack the preocular impression.

Strumigenys nidifex was originally assigned to the *szalayi* group by Brown (1971), but recent molecular analysis suggests instead that it is a member of the in situ Fijian radiation (Booher and Economo, unpublished data). Mann (1921) discovered colonies containing upwards of 100 individuals and noted that the workers build thin walls of mud throughout the nest to separate small chambers. E.O. Wilson collected a colony from Viti Levu during his expedition to Fiji and sent it back to Brown's laboratory in the United States.

Brown (1971) reported that the colony of 70–80 workers and several dealates was kept for 2 yr. The colony was easy to keep and produced broods of males and queens three times in 2 yr. The workers captured and fed to their larvae a wide variety of small arthropods, including mosquitoes, *Drosophila*, mites, aphids, beetles, blattarian nymphs, geophilomorph centipedes, and collembola. Brown also discussed predatory, defensive, and oviposition behavior. *Strumigenys nidifex* is thus one of the very few native Fijian *Strumigenys* for which any detailed natural history is known (Sarnat and Economo 2012).

S. oasis n. sp.

(Fig. 8C, D; Fig. 10E, F; Fig. 21; Fig. 27, Model 5)

(LSID: urn:lsid:zoobank.org:act:AD9D9AD1-CD62-49F3-91F5-28589BB2988B)

HOLOTYPE. Fiji, Viti Levu, Namosi Prov., near Nabukavesi Village, 2003-07-16, 300m, −18.1167° 178.2500°, primary rainforest, sifted litter, A. Rakabula (worker, dry pinned, BPBM, specimen code CASENT0185751). PARATYPES (same data as holotype): 1 worker (CASENT0185843, USNM), 1 worker (CASENT0185576, USNM, head only).

= *Strumigenys* sp. FJ19 (Sarnat and Economo 2012: 136, pl. 141)

Cybertype. Volumetric raw data (in DICOM format) of the physical holotype (CASENT0185751) is deposited at Dryad (https://doi.org/10.5061/dryad.1f9d55b/5) and can be freely accessed as virtual representation of the type. In addition to the cybertype data at Dryad, we also provide a freely accessible 3D surface model of the holotype at Sketchfab (https://skfb.ly/6vsIS).

Measurements (*n* = 2): TL 2.38–2.42 mm, HL 0.68–0.72 mm, HW 0.57–0.60 mm, CI 83–84, MdL 0.11 mm, MI 16, SL 0.31–0.35 mm, SI 44–45, PW 0.33 mm, PI 55–58, FL 0.31–0.35 mm, FI 52–61, EL 0.33 mm. Color polished reddish brown with yellow appendages. Head cordate, shield-like, becoming very broad posteriorly. Median of posterior head margin with distinct and deeply excavated circular pit. Mandibles strongly truncated and arcuate; shorter than length of terminal antennal segment. Apical fork comprised of three teeth; apical-most two teeth half the length as the third. In addition to the aforementioned three teeth is the basal-most fourth tooth, equal in length to the third, that is apparently homologous to the preapical tooth of relative species but here located so far distally as to be contiguous with the apical fork. Apicoscrobal hair thing stiff and straight. Ground pilosity of cephalic dorsum composed of short and appressed weakly spatulate hairs. Clypeal shield distinct and covered by closely spaced appressed spatulate hairs. Antennal scapes proportionally short (SI 44–45). Pronotal humeral hairs long, straight, and stiff. Surface of entire body strongly polished, entirely lacking sculpture except for short basigastral costulae. Dense tuft of white filamentous hairs arising from the lateral promesonotal border above the procoxae. Dorsal surfaces of mesosoma and metasoma with abundant long, stiff, erect hairs. Legs with abundant hairs similar to those on dorsal surfaces of body but entirely lacking flagellate hairs. Propodeal tooth short, broadly triangular. Propodeal lamella in profile with strongly convex posterior margin. In dorsal view, petiolar node distinctly broader than long. Ventral lobe of postpetiole large and broad, more lamellate than spongiform. Posterodorsal lobe of postpetiole obliquely costate, similar in pattern to basigastral sculpture.

Strumigenys oasis is without doubt the most peculiar representative of the genus in Fiji. The strongly truncated and arcuate mandibles with four spiniform apical teeth are unlike any other *Strumigenys* in Fiji—and possibly unique across the entire genus. They appear descended from an ancestor with long and linear mandibles rather than one with triangular mandibles armed with denticles. Another feature apparently unique to *S. oasis* is the circular pit excavated from the middle of the posterior head margin (Fig. 21D). While similar structures are observed in the species of other genera to receive ocelli, this does not appear to be the case for *S. oasis*. The third most anomalous feature of *S. oasis* is the dense tuft of white filamentous hairs arising from the lateral promesonotal border above the procoxae. Though homologous invaginations occur in many of the Fijian *Strumigenys* species, none are so deep or so densely covered in hairs as that of *S. oasis*. The only Fijian *Strumigenys* species approaching *S. oasis* in morphology is *S. basiliska*. Both are strongly polished and have short and curved mandibles with spiniform teeth, but those of *P. basiliska* are distinctly longer than those of *S. oasis*. Additionally, *P. basiliska* lacks the median pit on the posterior head margin, shield-shaped head, propodeal lamellae, and abundant long, stiff, erect hairs. The only collection of this species is from a leaf litter sample taken at Nabukavesi in southeastern Viti Levu.

Etymology: Oasis (Ontologically Anthropocentric Sensory Immersive Simulation) refers to the virtual reality world featured in the fictional work *Ready Player One* (Cline 2011). The name is a noun in apposition and thus invariable.

S. panaulax Bolton

([Fig. 8E](); [Fig. 10G](), H; [Fig. 27]())

panaulax. Strumigenys panaulax [Bolton 2000](): 811; worker described. Type locality: FIJI, Vanua Levu, Ndelaikoro, 800 m., 27.x.1977, litter, No. 77/130 (G. Kuschel). HOLOTYPE: (ANIC, examined). PARATYPEs: (ANIC, BMNH, not examined). *Nec* [Sarnat and Economo 2012]() (material refers instead to *parzival*).

Worker. Measurements (*n* = 4). 2.1–2.2, HL 0.52–0.56, HW 0.38–0.40, CI 71–74, MdL 0.24–0.26, MI 46–47, SL 0.30–0.32, SI 79–80, PW 0.24–0.25. *Strumigenys panaulax* is a long-mandible, small reddish-brown species covered with thick decumbent hairs and with uniform costulae that extend across the entire length of the first gastral segment. The combination of obliquely oriented costulae on the pronotal dorsum and sides, transverse costulae on the petiolar dorsum, and longitudinal costulae on the postpetiolar disc and across the first gastral tergite is entirely unique among Fijian *Strumigenys*. The apicoscrobal, pronotal humeral, and basitarsal hairs are all flagellate. The propodeal lamella has a straight posterior margin in profile view. The only other Fijian *Strumigenys* with such distinctive gastral sculpture is *S. parzival*. Whereas the dorsal surfaces of the pronotum and petiole are obliquely costulate-rugulose in *S. panaulax*, those of *S. parzival* are irregularly rugoreticulate and oriented longitudinally. The specimens referred to and figured in [Sarnat and Economo (2012)]() as *S. panaulax* are considered here as belonging to *S. parzival*.

S. parzival n. sp.

([Fig. 8F](); [Fig. 10I](), J; [Fig. 22](); [Fig. 28](), [Model]() 6)

(Zoobank LSID: urn:lsid:zoobank.org:act:AFDB3FC1-822E-4EB2-B964-BC492CFD4F89)

HOLOTYPE. Fiji, Vanua Levu, 0.6 km S Rokosalase Village, 2005-05-11, 180m, −16.5332° 179.0180°, secondary forest, sifted litter, E.P. Economo, EPE92.07 (worker, dry pinned, BPBM, specimen code CASENT0186960). PARATYPE (same data as holotype): 1 worker (CASENT0186830, USNM). Misidentified as *S. panaulax* Bolton ([Sarnat and Economo 2012](): 132, pl. 130).

Cybertype. Volumetric raw data (in DICOM format) of the physical holotype (CASENT0186960) is deposited at Dryad ([https://doi.org/10.5061/dryad.1f9d55b/6]()) and can be freely accessed as virtual representation of the type. In addition to the cybertype data at Dryad, we also provide a freely accessible 3D surface model of the holotype at Sketchfab ([https://skfb.ly/6wMpx]()).

Worker. Measurements (*n* = 2): TL 2.10–2.24 mm, HL 0.51–0.54 mm, HW 0.39–0.40 mm, CI 74–77, MdL 0.23–0.24 mm, MI 45, SL 0.32–0.34 mm, SI 74–75, PW 0.24–0.25 mm, PI 60–63, FL 0.32–0.34 mm, FI 82–84, EL 0.24–0.25 mm. Color dull dark reddish-brown with yellowish-brown appendages. Color dark reddish-brown. Mandibles long and linear with one preapical tooth; preapical tooth length approximate to maximum mandible width. Apicoscrobal hair filiform to flagellate. Cephalic dorsum uniformly reticulate-punctate. Ground pilosity of cephalic dorsum short, simple, strongly curved. Pronotal humeral hairs flagellate. Pronotal dorsum longitudinally and irregularly rugoreticulate; mesonotum reticulate-punctate; propodeal dorsum and declivity polished smooth. Side of pronotum longitudinally costulate. Mesopleuron, metapleuron, and side of propodeum polished smooth. Pronotal dorsum with one pair and mesonotum with

one to two pairs of erect flagellate hairs; ground pilosity long, curved, and flexous. Dorsal surface of hind tibia with at least one flagellate hair that is similar to that on the basitarsus. Propodeal tooth short, narrowly triangular. Propodeal lamella in profile with a straight to shallowly convex posterior margin. Petiolar node in profile evenly convex with similar anterior and posterior faces; lateral spongiform lobe small; restricted to posterior margin of node. Dorsum of petiole strongly reticulate-punctate. Postpetiolar disc weakly reticulate-punctate. Ventral lobe of postpetiole large, thin, and more lamellate than spongiform. Dorsum of petiolar node rugoreticulate; disc of postpetiole with closely spaced longitudinal costulae. First gastral tergite with closely spaced broad and uniform costulae that extend unbroken from base to apex. First gastral tergite with sparse erect flagellate hairs and long filiform pilosity.

Strumigenys parzival is a small dark reddish-brown species with flagellate apicoscrobal, humeral and basitarsal hairs, but is most recognizable by the uniform costulae that extend longitudinally across the entire first gastral tergite. The species is nearly identical to *P. panaulax* with respect to both pilosity patterns and the gastral sculpture. The two are so similar that [Sarnat and Economo (2012)]() did not recognize *S. parzival* as a new species distinct from *P. panaulax*. Subsequent comparison with the type specimen of *P. panaulax* revealed discrete differences between the two species with respect to pronotal and petiolar sculpture. Whereas the pronotal dorsum and petiolar dorsum of *P. panaulax* are obliquely costulate-rugulose, those of *P. parzival* are longitudinally and irregularly rugoreticulate. Both these ants are similar to a cluster of species closely related to *S. chernovi*, and additional diagnostic notes are listed under the latter. *Strumigenys parzival* is known only from a single leaf litter collection of two workers on Vanua Levu.

Etymology: Parzival refers to the name of the protagonist's virtual reality avatar in the fictional work *Ready Player One* ([Cline 2011]()). The name is a noun in apposition and thus invariable.

S. praefecta Bolton

([Fig. 8G](); [Fig. 10K](), L; [Fig. 23](); [Fig. 28]())

praefecta. Strumigenys praefecta [Bolton 2000](): 826; worker, queen described. Type locality: FIJI, Viti Levu, Namosi/Queens Rd Divide, 23.vii.1987, QM Berlesae No. 787, 18°05′S, 178°10′E, 500 m., rainforest, litter and moss (G. Monteith). HOLOTYPE: worker (ANIC, examined). PARATYPEs: (ANIC, examined); worker (BMNH, examined). In Fiji ([Sarnat and Economo 2012](): 132, pl. 131).

Worker. Measurements (n= 4): TL 2.5–2.6, HL 0.66–0.70, HW 0.42–0.45, CI 64, MdL 0.30–0.32, MI 45–46, SL 0.42–0.44, SI 95–100, PW 0.26–0.28. *Strumigenys praefecta* is a long-mandible, mid-sized dark, reddish-brown species with very short antennal scrobes, simple apicoscrobal hairs, no pronotal humeral hairs, and no flagellate basitarsal hairs. Among long-mandible Fijian *Strumigenys*, the only other species lacking pronotal humeral hairs is *S. sulcata*. Whereas *S. praefecta* is characterized by the same finely reticulate-punctate sculpture present in so many of the Fijian *Strumigenys*, the deeply rugose-sulcate sculpture of *S. sulcata* is quite distinct and even occurs on the mesopleuron. [Bolton (2000)]() and [Sarnat and Economo (2012)]() reported morphological variation across populations o *S. sulcata* in Fiji, but we find no compelling evidence for treating these as separate species.

Strumigenys praefecta may be arboreal, as much of the examined material was collected from under moss on trees, under bark on trees, foraging on tress, and from canopy fogging.

S. rogeri Emery

([Fig. 8H](); [Fig. 10M](), N; [Fig. 28]())

rogeri. Strumigenys rogeri Emery 1890: 68, pl. 7, [Fig. 6](); worker described. Type locality: ANTILLES IS., St. Thomas I. [not examined]. Queen described ([Forel 1893](): 378). Senior synonym of *incisa* ([Donisthorpe 1915](): 341); of *sulfurea* ([Brown 1954](): 20). In Afrotropical revision ([Bolton 1983](): 387); global revision ([Bolton 2000](): 604); Polynesia ([Wilson and Taylor 1967](): 39). In Fiji ([Sarnat and Economo 2012](): 133).

incisa. Strumigenys incisa [Godfrey 1907](): 102 [attributed to Forel] (w.) GREAT BRITAIN, Scotland, Edinburgh, hothouse in Royal Botanic Garden, 10.vi.1904 (*R. Godfrey*). Junior synonym of *rogeri*: [Donisthorpe 1915](): 341.

sulfurea. Strumigenys sulfurea Santschi 1915: 261 (w.) GABON, Samkita (*F. Faure*). Junior synonym of *sulfurea* ([Brown 1954](): 20).

Worker. Measurements (n = 40): TL 2.3–2.8, HL 0.58–0.74, HW 0.42–0.52, CI 69–75, MdL 0.31–0.40, MI 51–58, SL 0.36–0.46, SI 82–89, PW 0.27–0.32. *Strumigenys rogeri* is a light yellow-brown species that can be immediately identified by its preocular notch on the ventrolateral margin of the head, two preapical teeth on the mandibles, and small size. No other *Strumigenys* species in Fiji has two preapical teeth. The only other *Strumigenys* in Fiji with any preocular indentation approaching that of *S. rogeri* are *S. nidifex* and its close relation, *S. avatar*. The latter two species are both very large, dark, long-limbed, heavily punctate species with a single preapical tooth on the mandible. *Strumigenys rogeri* is a tramp species believed to be native to Africa and is widespread across Fiji.

S. scelesta Mann

([Fig. 8I](); [Fig. 10O](), P; [Fig. 28]())

scelesta. Strumigenys scelestus [Mann 1921](): 463, [Fig. 22b](); worker described. Type locality: FIJI, Taveuni, in mountains near lake [Lake Tagimaucia] (W. M. Mann). HOLOTYPE [single specimen]: worker (USNM, examined). In global revision ([Bolton 2000](): 812). In Fiji ([Sarnat and Economo 2012](): 133, pl. 133).

Worker. Measurements (*n* = 1). TL 2.3, HL 0.57, HW 0.42, CI 74, MdL 0.21, MI 37, SL 0.32, SI 76, PW 0.25. *Strumigenys scelesta* is a small, long-mandible, light reddish-brown species with a dense covering of short subdecumbent hairs on all of its dorsal surfaces, a flagellate basitarsal hair, no projecting apicoscrobal or pronotal humeral hairs, and a broad propodeal lamella. The species was described by [Mann (1921)]() from the single holotype which is in rather poor condition. It is therefore difficult to comment on the specialized hairs, which could either be naturally absent or worn off by damage. However, the 2002–2008 survey recovered several specimens that bear close resemblance to *S. scelesta*. We follow the decision by [Sarnat and Economo (2012)]() to, with reservation, consider those specimens as belonging to *S. scelesta*. A more thorough discussion of the differences between the specimens in question and the holotype was given in the aforementioned study. *Strumigenys scelesta* is best diagnosed by the combination of the following three characters: presence of flagellate basitarsal hair, absence of projecting apicoscrobal hair, absence of projecting pronotal humeral hair. No other species of Fijian *Strumigenys* has all three characters. The specimens considered here to be *S. scelesta* were collected from the lower elevations of Vanua Levu and Viti Levu.

S. sulcata Bolton

([Fig. 8J](); [Fig. 10Q](), R; [Fig. 24](); [Fig. 28]())

sulcata. Strumigenys sulcata [Bolton 2000](): 828; worker, queen described. Type locality: FIJI, Vanua Levu, Nedreketi [= Dreketi], 25.x.1977, litter, wood, No. 77/127 (G. Kuschel). HOLOTYPE: worker (ANIC, not examined). PARATYPEs: (ANIC, not examined); worker (BMNH, examined). In Fiji ([Sarnat and Economo 2012](): 134, pl. 134).

Worker. Measurements (*n* = 5). TL 3.6–3.8, HL 0.92–1.00, HW 0.65–0.74, CI 68–74, MdL 0.44–0.48, MI 46–49, SL 0.58–0.64, SI 87–94, PW 0.41–0.47. *Strumigenys sulcata* is a relatively large, long-mandible, dark reddish-brown species with the dorsal surfaces of the mesosoma and postpetiole deeply sulcate. The species lacks projecting apicoscrobal hairs, pronotal humeral hairs, basitarsal hairs, and propodeal lamellae. The rugae of the dorsum of head and sides of mesosoma are also primarily longitudinal, but less regular and more reticulated. The petiole lacks a distinct node. Instead, the peduncle arches gradually into the posterior margin. The only other long-mandible Fijian *Strumigenys* that entirely lacks freely projecting hairs is *S. praefecta*. The two species are easily distinguished from each other by the sculpture, however, with *S. sulcata* deeply sulcate and rugose and *S. praefecta* finely reticulate-punctate. *Strumigenys sulcata* is known from most of the archipelago's major islands, and nests have been found in wet, decaying logs.

S. trauma (Bolton)

([Fig. 8K](); [Fig. 10S](), T; [Fig. 28]())

trauma. Pyramica trauma [Bolton 2000](): 408; worker described. Type locality: FIJI, Kadavu, Mt. Korogatule, nr. Matasawalevu, 18°59′S, 178°28′E, 4.vii.1987, 300 m., rainforest sieved litter, QM Berlesate No. 773 (G. Monteith). HOLOTYPE: worker (ANIC, examined). PARATYPE: worker (BMNH, not examined). Combination in *Strumigenys*: [Baroni Urbani & De Andrade 2007](): 129. In Fiji ([Sarnat and Economo 2012](): 118, pl. 115).

= *Pyramica* sp. FJ02 ([Sarnat and Economo 2012](): 119, pl. 116)

Worker. Measurements (n = 5). TL 1.87–2.44, HL 0.49–0.62, HW 0.39–0.49, CI 79–81, MdL 0.09–0.15, MI 19–23, SL 0.31–0.42, SI 59–63, PW 0.26–0.31, PI 63–71, FL 0.31–0.42, FI 80–86, EL 0.26–0.31. *Strumigenys trauma* is a short-mandible, dark brown species with two pairs of standing cephalic hairs, long stout pronotal humeral hairs, punctate dorsal surfaces of the mesosoma and petiole, and a very broad postpetiolar disc. The only other short-mandible *Strumigenys* currently known from Fiji is the tramp *S. membranifera* which is separated from *S. trauma* by the lack of pronotal humeral hairs and the smooth dorsal surfaces of its mesosoma and petiole. After reviewing the material designated as *Pyramica* sp. FJ02 (= *Strumigenys*) by [Sarnat and Economo (2012)]() we decide here to include it in a broader definition of *S. trauma*. While the specimens in question differ from the type material with respect to larger size, smoother pronotal sculpture, and coarser basigastral sculpture the lack of sympatry between the morphological variants and general weakness of the differences leads us to consider the variation as be populaiton-level rather than heterospecific, though additional sampling or analysis could provide evidence to the contrary. This species was assigned by [Bolton (2000)]() to the *capitata* group, and is presumed to be closely related to *S. charybdis* (Indonesia), *S. epipola* (Samoa), *S. phasma* (New Guinea), *S. tethys* (New Guinea) and *S. themis* (New Guinea).

S. tumida Bolton

([Fig. 8L](); [Fig. 10U](), V; [Fig. 25](); [Fig. 28]())

tumida. *Strumigenys tumida* Bolton 2000: 830; worker, queen described. Replacement name for *Strumigenys wheeleri* Mann 1921: 466, Fig. 24. Type locality: FIJI, Viti Levu, Nadarivatu (W. M. Mann). Syntypes: 2 workers, 1 queen (MCZC type no. 23319, examined). In Fiji (Sarnat and Economo 2012: 135, pl. 135).

wheeleri. *Strumigenys wheeleri* Mann 1921: 466, Fig. 24. Junior secondary homonym of *Epitritus wheeleri* Donisthorpe 1916: 121 (now in *Strumigenys*).

Worker. Measurements (*n* = 2): TL 3.8, HL 1.02, HW 0.65–0.69, CI 64–68, MdL 0.44, MI 43, SL 0.66, SI 96–102, PW 0.44–0.46. *Strumigenys tumida* is a long-mandible, dark brown, strongly sculptured species with freely projecting apicoscrobal and pronotal humeral hairs and no flagellate basitarsal hair. With respect to size and overall shape *S. tumida* is closest to *S. praefecta* and *S. sulcata*, but can be distinguished from those species by the presence of projecting humeral hair, the much broader postpetiole relative to the petiole, distinctly short preapical tooth on the mandible, and extremely swollen postpetiole which is conspicuously twice as broad as the petiole in dorsal view. *Strumigenys tumida* is known from forest habitats most of Fiji's largest islands except for Kadavu.

Acknowledgments

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