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Orsonwelles, a new genus of giant linyphiid spiders (Araneae) from the Hawaiian Islands

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Abstract. The Hawaiian spider genus *Orsonwelles*, gen. nov. (Araneae:Linyphiidae) is described. All *Orsonwelles* species are single island endemics: Kauai harbours six species; Oahu has three; Molokai has two; and Maui and Hawaii have one species each. The thirteen species included in *Orsonwelles* are described and illustrated: *O. torosus* (Simon), comb. nov., *O. malus*, sp. nov., *O. calx*, sp. nov., *O. ventus*, sp. nov., *O. bellum*, sp. nov. and *O. iudicium*, sp. nov. from Kauai; *O. polites*, sp. nov. (the type species), *O. ambersonorum*, sp. nov. and *O. arcanus*, sp. nov. from Oahu; *O. othello*, sp. nov. and *O. macbeth*, sp. nov. from Molokai; *O. falstaffius*, sp. nov. from Maui; and *O. graphicus* (Simon), comb. nov. from Hawaii. A total of 55 morphological characters (plus one behavioural character) were scored for twelve taxa (four *Orsonwelles* species plus eight linyphiid outgroups) to test the monophyly of the genus using cladistic methods. The most parsimonious cladograms provide robust character support for the monophyly of *Orsonwelles*. A single colonisation of the Hawaiian archipelago is hypothesised to explain the presence of these species in the Hawaiian Islands. This genus represents a case of insular gigantism (these are the largest linyphiids described), although the close relatives of *Orsonwelles* remain unknown. Their web architecture is also described and illustrated.

Introduction

The genus *Orsonwelles* groups the members of a recently discovered radiation of spiders from the Hawaiian Islands. These linyphiids are remarkably large (a genuine case of insular gigantism) and exhibit distinctive patterns of endemism, typical of many Hawaiian taxa (Carlquist 1980; Howarth and Mull 1992). Species of *Orsonwelles* are some of the most conspicuous native arthropod predators of Hawaiian wet and mesic forests. Most of the species of this new genus are described here for the first time.

Hawaiian natural history

The extreme isolation of the Hawaiian archipelago has resulted in one of the most remarkable oceanic island biotas (Carlquist 1980, 1995). Hawaii is the most isolated major island group in the world, it is located about 4000 km away from the nearest continental land mass (North America) and more than 1600 km away from the nearest island group (Line Islands) (Simon 1987). The terrestrial biota of the Hawaiian Islands is the result of dispersal from many different parts of the world (Wagner and Funk 1995). Some of the best-known animal radiations include the Hawaiian honeycreepers (Freed *et al.* 1987; Tarr and Fleischer 1995), land snails (Cowie *et al.* 1995) and several groups of terrestrial

arthropods. The radiations of terrestrial arthropods in the Hawaiian Islands are particularly impressive because of the extremely high proportion of endemics (around 98-100% for almost all groups of arthropods that are native to the islands; Carlquist 1980; Howarth 1990; Howarth and Mull 1992; Wagner and Funk 1995). These radiations include, among others, drosophilid flies (Carson and Kaneshiro 1976; DeSalle and Hunt 1987; DeSalle 1992), crickets (Otte 1994; Shaw 1995, 1996a, 1996b), mirid bugs (Asquith 1994a, 1994b, 1995), planthoppers (Asche 1997; Roderick 1997), damselflies (Polhemus and Asquith 1996; Polhemus 1997), carabid beetles (Liebherr 1995, 1997, 2000; Liebherr and Zimmerman 1998), cerambycid beetles (Gressit 1978) and tetragnathid spiders (Gillespie 1991a, 1991b, 1992a, 1992b, 1993, 1994; Gillespie et al. 1994; Gillespie and Croom 1995; Gillespie et al. 1997).

Island biotas have played a major role in the development of the evolutionary paradigm. The Hawaiian Islands offer an unparalleled opportunity to study evolutionary patterns of species diversification because of their exceptional geographic position. The isolation of the archipelago has resulted in a truly unique terrestrial biota, characterised by a large number of species that represent a relatively small number of species-groups (Simon 1987). Unfortunately, a large fraction of the biodiversity of the archipelago remains unknown and undocumented (Eldredge and Miller 1995; Miller and Eldredge 1996). This is particularly tragic given the ecological fragility of the few remaining native habitats. Hawaii has indeed acquired the less distinguished reputation of being a hot bed of extinction (Mlot 1995).

The geological history of the Hawaiian Islands is relatively well understood (Stearns 1985; Carson and Clague 1995). The chronology of the islands is well known from potassium-argon and magnetic declination data and provides a basis for dating some of the macroevolutionary patterns. The Hawaiian Islands were formed successively over a fixed volcanic hot spot beneath the north-westward-moving Pacific tectonic plate. The prevailing physical model suggests a thermal plume of material that arises at the mantle and forms a melting anomaly beneath the plate. As the tectonic plate moves over the hot spot, the magma perforates the plate at intervals and forms volcanoes. These volcanoes, initially below sea level, may emerge as oceanic islands (Wilson 1963; references in Carson and Clague 1995). As a consequence, the Hawaiian Islands are arranged linearly in chronological order. Nihau and Kauai are the oldest of the current large, high islands (c. 5.1 million years old). Oahu is about 3.7 million years old and is located south east of Kauai. Molokai, Maui, Lanai and Kahoolawe (0.8 to 1.9 million years) are situated on a common platform and were at some point connected above sea level, forming the so-called 'Maui Nui complex'. Hawaii, the youngest island (less than half a million years old), is located over the hot spot and still has active volcanoes. This chain is continued north-west of the current eight high islands by several lower islands and atolls and a series of submerged seamounts.

Hawaiian colonisation patterns

The Hawaiian Islands have been colonised almost exclusively by waif elements. Their isolation makes repeated colonisation by the same species unlikely (Wagner and Funk 1995). The biota of the Hawaiian Islands is primarily depauperate and secondarily enriched (Mueller-Dombois 1981). Although depauperate at the genus and family levels, this is made up for at the species level, giving approximately the numbers of species that one would expect for the size of the island (at least for groups that have been well studied, such as plants). A large fraction of the plant and animal species in the Hawaiian Islands are the result of colonisation events from the Indo-Pacific region, only a few have New World affinities. The biogeographic patterns of Hawaiian taxa often suggest a single ancestral colonisation event followed by subsequent speciation and radiation in the islands, though it has not been possible to determine the source of the colonists in many cases. Phylogenetic hypotheses of Hawaiian taxa, and the biogeographic implications derived from them, can be contrasted with the geological history of the archipelago. Funk and Wagner (1995) compared the biogeographic patterns of 19 lineages

of plants and terrestrial animals and found that dispersal from older to younger islands (progression), single island (or volcano) radiations and sequential radiations were the most frequent patterns. They also found that speciation occurred more often within islands than between islands (two thirds versus one third respectively). Roderick and Gillespie (1998*a*) have recently provided an overview of patterns of differentiation among arthropods in the islands.

Hawaiian Araneae

There have been many studies of spider insular faunas, though most of them only document the taxa that are found on the island or archipelago. These studies include the spider faunas of Macaronesia (main references in Wunderlich 1987, 1991; Arnedo and Ribera 1996, 1997, 1999; Arnedo et al. 1996, 2000), the Galapagos Islands (numerous papers by Baert and collaborators, e.g. Baert et al. 1989), Saint Helena (several references by Benoit, e.g. Benoit 1977; van Helsdingen 1977; Hormiga 1998), Comoro (Jocqué 1985), Seychelles (several references by Benoit, e.g. Benoit 1978, and Saaristo, e.g. Saaristo 1978), Krakatau (Bristowe 1931; Reimoser 1934), Micronesia and Polynesia (Berland 1934a, 1934b; 1942; Lehtinen 1980; Beatty et al. 1991), and the Hawaiian Islands (Simon 1900, 1904; Suman 1964, 1965, 1967, 1970; Gillespie 1991a, 1991b, 1992a, 1992b, 1993, 1994; Gillespie et al. 1994; Gillespie and Croom 1995; Gillespie et al. 1997).

The most comprehensive treatments of Hawaiian spiders to date have been Simon's (1900, 1904) contributions in Fauna Hawaiiensis. For most of twentieth century, Hawaiian spiders received relatively little attention in the taxonomic literature, with some notable exceptions such as the works of Suman (1965, 1970), Gertsch (1973) and Gillespie (1991a, 1992a, 1994). Suman (1964) and Gillespie et al. (1998) have summarised the history of araneology in Hawaii. The most speciose spider-group in Hawaii is the genus Tetragnatha (Tetragnathidae) (Simon 1900; Gillespie 1991a, 1992a, 1994), with 28 described species and more than 50 awaiting description (Gillespie et al. 1998). Other radiations include members of Theridion and Argyrodes (Theridiidae) (Simon 1900; Gillespie et al. 1998; M. Arnedo, personal communication), several groups within the families Thomisidae, Philodromidae and Salticidae (Simon 1900; Suman 1970; Gillespie et al. 1998; M. Arnedo, personal communication) and the so called Hawaiian 'Labulla', which are the subject of this study. In total, less than 200 species of spiders have been reported from the Hawaiian Islands (Nishida 1994). Although this number is clearly an underestimate, it suggests a relatively depauperate spider fauna compared to continental faunas or even to other oceanic islands (e.g. c. 430 species of spiders in the Canary Islands, Wunderlich 1991).

Native arthropod species have been largely extirpated from the low elevations (below 300 m) in the Hawaiian

Islands (Roderick and Gillespie 1998b). The levels of endemism currently reported for Hawaiian spiders (*c*. 60% in Nishida 1994, although non-native species were included in the calculation of this figure) are also an obvious underestimate. For example, addition of undescribed species of tetragnathids (Gillespie and Croom 1995; Gillespie *et al.* 1997; R. G. Gillespie, personal communication) and *Orsonwelles* raises the endemism rate to about 85%. Further study will most likely result in the discovery of new endemic species. Despite the high level of endemism, the Hawaiian fauna represents only a relatively small fraction of higherlevel spider diversity, with only about 15 of 109 spider families naturally occurring in the Hawaiian Islands (Howarth and Mull 1992).

In this paper I describe a newly discovered radiation of endemic Hawaiian linyphiid spiders. One of the most remarkable aspects of this work is the fact that, despite the conspicuousness of these spiders, most of the species (eleven out of thirteen) were previously undescribed and the radiation had not before been identified as such.

Taxonomic history

Only two members of Orsonwelles, O. torosus (Simon) and O. graphicus (Simon), have received attention in the taxonomic literature. Simon (1900) originally placed these two species in his genus Labulla Simon and stated (p. 462) that these two large species represented the genus Labulla in the Hawaiian Islands. Although he discussed how these two Hawaiian taxa differ from Labulla thoracica (Wider), the type species, in their somatic morphology, he did not explain why they should be included in Labulla. It should be noted that at that time, the genus Labulla also included the pimoid species Pimoa altioculata (Keyserling) and P. rupicola (Simon). From a modern perspective, it seems that Simon used the genus Labulla as a dumping ground for morphologically deviant linyphioids because Labulla, as it is currently delimited, is polyphyletic (Hormiga 1994a: 11). Two species from Japan and adjacent islands, Labulla contortipes (Karsch) and L. insularis (Saito), belong to a new genus in the family Pimoidae (Hormiga, unpublished data). Labulla nepula Tikader, from India, is not congeneric with the type species, L. thoracica, from Europe. Only two of the eight species currently classified in Labulla seem to be congeneric with L. thoracica, namely, L. flahaulti Simon (from France) and L. impudica Denis (from Algeria).

Despite the relatively large size, relative abundance and easy accessibility of at least some species of *Orsonwelles*, nothing had been published about these animals after Simon (1904) and only two of the thirteen species described in this revision bore Latin binomens.

Materials and methods

Very few specimens of *Orsonwelles* were available in museum collections. As a consequence, most of the specimens studied in this

monograph were collected during three one-month field trips that I carried out during 1995, 1999 and 2000. This has allowed me to study and collect specimens of all the species of *Orsonwelles*, with the exception of *O. torosus*, which I presume extinct (see later). A number of colleagues doing fieldwork in Hawaii were also kind enough to collect some additional animals for this revision. I have been able to document habitat, web architecture and a few natural history traits for almost all the species. Webs were dusted with cornstarch (Eberhard 1976; Carico 1977) and photographed with a Nikon 8008 s or F100 using a 60 mm macro lens and a speedlight. Webs were often located and flagged with biodegradable surveyor tape during the day to be able to find them again at night. The animals were collected at night and often kept alive for photography. All photographs (including those of webs) have associated voucher specimens. Subadult individuals were kept alive on small cups, housed in coolers, until they moulted.

Morphological methods of study follow those described in more detail in Hormiga (1994a, 2000). Specimens were examined and illustrated using a Leica MZAPO stereoscopic microscope with a camera lucida. Further details were studied using a Leica DMRM compound microscope with a drawing tube. Some microscope images were recorded using a Leica DC-200 digital camera. A LEO 1430VP Scanning Electron Microscope (SEM) was also used to study and photograph morphological features. Original SEM images were stored as high-resolution TIFF files (c. 3 megabytes). Scanning Electron Microscope images were adjusted and edited (contrast, brightness etc.) using Adobe Photoshop® and plates were composed and labelled electronically using Adobe Illustrator®. The final illustrations were rendered using technical pens on drafting film and Prismacolor® pencils and technical pens on coquille board (fine grain). Left structures (e.g. palps, chelicerae etc.) are depicted, but in a few instances the right structure is used (unless otherwise noted in the figure legend, the image of right structures is reversed to facilitate comparisons). Hairs and macrosetae are usually not depicted in the final drawings.

For the male palp, I have tried to illustrate an ectal, ventral and dorsomesal view for each species. In some instances one or more additional views (e.g. dorsal) were required to better understand palp morphology, resulting in a diversity of angles. In general, illustrating identical palpal orientations throughout all species does not usually work well, because the best view to show morphology of sclerites may vary slightly from species to species (depending on the morphology of the sclerites, slight rotation of parts etc). The same applies to SEM images. Sometimes it is not possible to obtain identical palpal orientations for the dissecting microscope (the specimen is immersed in alcohol) and the SEM (the specimen has been critically point dried) because the sclerites move slightly relative to each other during the drying process. As a result, similar orientations of drawings and SEM micrographs of the same species may look slightly 'different.' The embolic division was excised and illustrated from several angles, but in a few cases I did not have enough male specimens to do this dissection (and thus it is not uniformly illustrated for all species). This plethora of illustrations serves two main purposes: 1, it provides a detailed visual description of the morphology of these (mostly undescribed) taxa; and 2, it helps in understanding the morphological homologies coded in the character matrix for cladistic analysis. In addition, all these illustrations are primary data, and as such are available to be reused, reinterpreted or reassessed by any researcher (in an analogous way to nucleotide sequences stored at GenBank).

All morphological measurements are in millimetres. Somatic morphology measurements were taken using a scale reticle in the dissecting microscope. Eye diameters are taken from the span of the lens. Cephalothorax length and height were measured in lateral view and its width was taken at the widest point. Similarly, the length and height of the abdomen was measured in lateral view, and the width as the widest point as seen from a dorsal view. The measurements of the

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abdomen are only approximations because the abdomen size changes more easily in preserved specimens than other more sclerotised parts (e.g. the chelicerae). The total length was measured in lateral view and is also an approximation because it involves the size of the abdomen and its relative position. Approximate leg article lengths were measured in lateral view by perpendicular positioning of the article being measured without detaching the leg from the animal. The position of the metatarsal trichobothrium is expressed as in Denis (1949) and Locket and Millidge (1953). Female genitalia were excised using surgical blades or sharpened needles. The specimen was then transferred to methyl salicylate (Holm 1979) for examination under the microscope, temporarily mounted as described in Coddington (1983). Scale bars are given for all camera lucida drawings as an approximation of the relative size of the structures depicted.

Male palps that were examined with the SEM were first excised and transferred to a vial with 70% ethanol and then cleaned ultrasonically for one to three minutes. The specimen was then transferred to absolute ethanol and left overnight. After critical point drying, the specimens were glued to rounded aluminum rivets using an acetone solution of polyvinyl resin and then Au/Pd coated for examination at the SEM.

I followed the method described in Hormiga (1994*a*) for dissections of the tracheal system. Methods of study and homology assessments of spinneret spigot morphology follow those of Coddington (1989) and Hormiga (2000).

Unless otherwise stated, the studied specimens are deposited at the USNM collection (Smithsonian Institution) in Washington, D.C.

Abbreviations used in the text and figures

Male palp. A, Alveolus; BH, basal haematodocha; CB, cymbium; CL, column; DSA, distal suprategular apophysis; E, embolus; ED, ejaculatory duct; EM, embolic membrane; F, fundus; m, membrane (or membranous); LC, lamella characteristica; MCA, mesal cymbial apophysis; P, paracymbium; R, radix; RCA, retromarginal cymbial apophysis; SPT, suprategulum; ST, subtegulum; T, tegulum; TA, terminal apophysis; TS, terminal sclerite.

Epigynum. CD, Copulatory duct; CO, copulatory opening; DP, dorsal plate; FD, fertilisation duct; S, spermatheca; VP, ventral plate.

Somatic morphology. AC, Aciniform gland spigot(s); AG, aggregate gland spigot(s); ALS, anterior lateral spinneret; AME, anterior median eye(s); CY, cylindrical gland spigot(s); FL, flagelliform gland spigot(s); MAP, major ampullate gland spigot(s); mAP, minor ampullate gland spigot(s); PI, piriform gland spigot(s); PLE, posterior lateral eye(s); PLS, posterior lateral spinneret; PME, posterior median eye(s); PMS, posterior median spinneret.

Museum and research collections

AMNH	American Museum of Natural History, New York
BM	Bernice Bishop Museum, Honolulu
BMNH	The Natural History Museum, London
CAS	California Academy of Sciences, San Francisco
HAD	Hawaii Department of Agriculture, Honolulu
MNHN	Museum National d'Histoire Naturelle, Paris
OM	Otago Museum, Dunedin, New Zealand
USNM	Smithsonian Institution, Washington, D. C.
ZMUC	Zoological Museum, University of Coper

ZMUC Zoological Museum, University of Copenhagen, Copenhagen

Cladistic analysis

The cladistic analysis was designed to test the monophyly of *Orsonwelles* using a sample of four species and eight linyphiid outgroups in seven genera. In a separate publication (Hormiga *et al.* in press) the phylogenetic relationships of the thirteen *Orsonwelles* species are reconstructed using a

combination of morphological and molecular (DNA sequences from nuclear and mitochondrial genes) characters. Because of the highly autapomorphic morphology of Orsonwelles it is difficult to hypothesise what the close relatives of this radiation may be. I do not know of any linyphiid species that closely resembles any of the species of Orsonwelles. Male palpal morphology suggests that Orsonwelles belongs in the Linyphiini clade (Hormiga 2000), some of the palpal sclerites are somewhat similar to those of Neriene Blackwall (Blauvelt 1936; van Helsdingen 1969) but very different in detail (e.g. paracymbium or placement and morphology of terminal apophysis). The linyphiine outgroups sampled here are those used in Hormiga (2000), Microlinyphia Gerdhardt and Linyphia Latreille, with the addition of four more species: Labulla thoracica; costatus *Pityohyphantes* (Hentz); Neriene radiata (Walckenaer); and N. variabilis (Banks). The inclusion of L. thoracica will test the conjecture that the Hawaiian taxa are only distantly related to the type species of Labulla.

I have scored a total of 56 characters: 30 male and eleven female genitalic characters; 14 somatic morphological characters and one behavioural character (see Table 1). The parsimony analyses were performed using the computer programs Hennig86 version 1.5 (Farris 1988) and NONA version 2.0 (Goloboff 1993). WinClada version 0.9.99 m24 (Nixon 1999) and Nexus Data Editor 0.4.9 (Page 2001) were used to study character optimisations on the cladograms and to build and edit the character matrix respectively. Ambiguous character optimisations were usually resolved so as to favour reversal or secondary loss over convergence (Farris optimisation or ACCTRAN); if not, the optimisation scheme is discussed in the text. The 15 multistate characters were treated as non-additive (unordered or Fitch minimum mutation model, Fitch 1971). NONA was used to calculate Bremer support indices (BS) (Bremer 1988, 1994; Donoghue et al. 1992).

Characters

In this section I describe the characters used in the cladistic analysis (Table 1), grouped by 'Character Systems'. When necessary for clarity, examples of taxa exhibiting a particular character state are given in parentheses. Many of the characters used to resolve relationships among the outgroup taxa have been taken from my previous work on linyphild phylogenetics (Hormiga 1994*a*, 1994*b*, 2000). Only new characters are discussed in more detail in this section.

Male palpal morphology

Character 1. Male pedipalpal tibial length: 0, short (less than twice its width); 1, long (more than twice its width).

Character 2. Paracymbium morphology (Hormiga 2000): 0, a more or less flat plate (Hormiga 1994*b*, fig. 13A); 1, thin and finger-like (Hormiga 1994*b*, fig. 8A); 2, knob-like and rounded (Fig. 43*E*).

Bolyphantes luteolus	0 0 0 0 0 0 - 0 - 0 0 1 1 0 1 0 0 0 0 - 0 0 0 0
Tenuiphantes tenuis	$0\ 0\ 0\ 0\ 0\ -0\ -0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Labulla thoracica	$0\ 0\ 0\ 0\ 0\ 0\ -\ 0\ -\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ -\ 0\ -\ 0\ 0\ 1\ 0\ 0\ 1\ 1\ 1\ -\ 0\ 1\ 1\ 2\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Pityohyphantes costatus	$0\ 1\ 1\ 0\ 0\ 0\ -\ 0\ -\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ -\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Microlinyphia dana	$0\ 1\ 1\ 0\ 0\ 1\ -\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Linyphia triangularis	$0\ 1\ 1\ 0\ 0\ 1\ -\ 1\ 1\ 1\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Neriene radiata	$0\ 1\ 1\ 0\ 0\ 1\ -\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Neriene variabilis	$0\ 1\ 1\ 0\ 0\ 0\ -\ 1\ 1\ 0\ 1\ 1\ 0\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 1\ 1\ 0\ 1\ 0\ 0\ 0\ 0\ 1\ 0\ 0\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Orsonwelles malus	$1\ 2\ 1\ 1\ 1\ 2\ 1\ 1\ 0\ 1\ 0\ 1\ 1\ 0\ 1\ 1\ 0\ 1\ 1\ 0\ 1\ 1\ 1\ 2\ 2\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Orsonwelles calx	1 2 1 1 1 2 1 ? ? 1 0 1 1 1 0 1 1 1 0 1 1 0 1 0 0 1 1 1 1 1 0 1 0
Orsonwelles arcanus	$1\ 2\ 1\ 1\ 1\ 2\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 0\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 0\ 0\ 1\ 0\ 0\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\$
Orsonwelles polites	1 2 1 1 1 2 0 1 0 1 0 1 1 1 0 1 0 1 0 1

Character 3. Paracymbium apophyses (Hormiga 2000): 0, present; 1, absent.

Character 4. Retromarginal cymbial apophysis: 0, absent; 1, present (Fig. 43E).

Character 5. Cymbial orifice: 0, absent; 1, present (Fig. 41F).

Character 6. Distal end of tegulum: 0, round, not projecting (Hormiga 2000, plate 1A); 1, subtle to medium projection (Hormiga 2000, plate 7A); 2, elongate and projecting (Fig. 15B).

Character 7. Apex of elongate tegular projection: 0, round (Fig. 31*B*); 1, pointed (Fig. 15*B*).

Character 8. Suprategular base: 0, approximately the same width as the rest of suprategulum; 1, enlarged (Fig. 25E).

Character 9. Suprategular base enlargement: 0, flat (Fig. 25E); 1, with depression (van Helsdingen 1969, fig. 164).

Character 10. Suprategular ectal margin: 0, thick (Hormiga 1994b, fig. 12); 1, thin or membranous (Fig. 25E).

Character 11. Embolus base (van Helsdingen 1969); 0, broad (Fig. 23F); 1, narrow (Hormiga 1994b, fig. 11).

Character 12. Apical half of embolus (Hormiga 2000): 0, filiform (Hormiga 1994b, fig. 12); 1, not thread-like (Fig. 23F).

Character 13. Embolic membrane (Hormiga 2000): 0, absent; 1, present (Fig. 43C).

Character 14. Column position on suprategulum (Hormiga 2000): 0, distal (Hormiga 1994b, fig. 14); 1, proximal (Fig. 23D).

Character 15. Fickert's gland (Hormiga 1994b, fig. 14): 0, absent; 1, present.

Character 16. Terminal apophysis position: 0, apicalectoventral (van Helsdingen 1969, fig. 322, 323); 1, mesal (Fig. 23*C*); 2, ectal (Merrett 1963, fig. 33).

Character 17. Terminal apophysis size: 0, small (Hormiga 1994b, fig. 12); 1, large, approximately same size as lamella (Fig.15C); 2, tiny (Hormiga 1994b, figs. 10, 11).

Character 18. Terminal apophysis shape: 0, entire (Hormiga 1994b, figs. 10, 11); 1, tri- or tetralobed (Fig. 23E).

Character 19. Terminal apophysis coiling: 0, not coiled (Fig. 23*E*); 1, spirally coiled (Hormiga 1994*b*, figs. 8, 9).

Character 20. Terminal apophysis apical process: 0, pointed (Fig. 44D); 1, round (Fig. 15G).

Character 21. Terminal sclerite (van Helsdingen 1969): 0, absent; 1, present (Figs 23F, 44B). Neriene variabilis lacks the terminal sclerite (Hormiga, unpublished data).

Character 22. Transversal sclerite: 0, absent; 1, present. The transversal sclerite (van Helsdingen 1969), found in some Neriene species, is present in N. radiata (Hormiga, unpublished data) as a small sclerite surrounded by membranous tissue and located between the membranous connection of the lateral projection of the lamella and the terminal sclerite. Van Helsdingen (1969, p. 134) describes the transversal sclerite of N. variabilis.

Character 23. Lamella characteristica (Hormiga 2000): 0, small (Hormiga 1994b, fig. 12); 1, large (Fig. 23A).

Character 24. Ectal process of lamella characteristica: 0, flat, thin or membranous (blade-like) (Hormiga 1994b, fig. 12); 1, thick (round section) (Fig. 15G); 2, blunt (van Helsdingen 1969, fig. 322).

Character 25. Striated area of lamella characteristica: 0, long (at least three times longer than wide) (Fig. 39B); 1, short (less than three times longer than wide) (Fig. 50C).

Character 26. Mesal tooth of lamella characteristica: 0, absent; 1, present (Fig. 23E).

Character 27. Mesal tooth of lamella characteristica size: 0, small (van Helsdingen 1969, fig. 322); 1, large (Fig. 23E).

Character 28. Mesal tooth of lamella characteristica position: 0, medial (open curve at lamella base; van Helsdingen 1969, fig. 320); 1, basal (more closed curve; Fig. 25D).

Character 29. Prolateral trichobothria on male pedipalpal tibia (Hormiga 2000): 0, one; 1, three; 2, four.

Character 30. Retrolateral trichobothria on male pedipalpal tibia (Hormiga 2000): 0, two; 1, three; 2, four or more.

Female epigynal morphology

Character 31. Epigynal dimension (ventral view): 0, longer than wide (Fig. 16B); 1, as wide as long or wider (Fig. 24A).

Character 32. Epigynum caudal region (ventral view): 0, straight–round (Fig. 28*A*); 1, V-shaped (Fig. 18*B*).

Character 33. Dorsal plate scape (Hormiga 2000): 0, absent; 1, present.

Character 34. Ventral plate scape (Hormiga 2000): 0, absent; 1, present.

Character 35. Dorsal plate epigynal socket (Hormiga 2000): 0, present (Fig. 40*E*); 1, absent.

Character 36. Median epigynal septum: 0, absent; 1, present.

Character 37. Epigynum lateral edge: 0, curved (Fig. 16*B*); 1, straight (Fig. 24*A*).

Character 38. Dorsal plate incision: 0, absent (Fig. 16*C*); 1, present (Fig. 24*B*).

Character 39. Atrium (Hormiga 2000): 0, absent; 1, present.

Character 40. Copulatory duct turning point: 0, absent (Fig. 24*E*); 1, present (van Helsdingen 1969, fig. 321).

Character 41. Fertilisation duct orientation: 0, posterior (van Helsdingen 1969, fig. 321); 1, mesal (Figs 16*F*, 24*E*); 2, anterior. The ducts are oriented anteriorly in *Labulla thoracica* (Hormiga, unpublished data; Millidge's illustration (1993, fig. 10) is not accurate).

Somatic morphology

Character 42. PME: 0, not on black tubercles or without entire black rings; 1, on black tubercles.

Character 43. Male chelicerae (Hormiga 2000): 0, smooth; 1, with stridulatory striae.

Character 44. Cheliceral stridulatory striae (Hormiga 2000): 0, ridged; 1, scaly.

Character 45. Prolateral teeth in female chelicerae: 0, six or less; 1, 9–13; 2, 14–15; 3, 16 or more.

Character 46. Retrolateral teeth in female chelicerae: 0, six or less; 1, 7–9; 2, ten or more.

Character 47. Prolateral teeth in male chelicerae: 0, five or less; 1, 9–11; 2, 12–14; 3, 15 or more.

Character 48. Retrolateral teeth in male chelicerae: 0, five or less; 1, 7–9; 2, ten or more.

Character 49. Retrolateral spines tibia III (female): 0, none; 1, one or more.

Character 50. Retrolateral spines tibia IV (female): 0, none; 1, one or more.

Character 51. Femur II–IV spines: 0, absent; 1, present. *Character 52.* Femur II dorsal spines (female): 0, three or less; 1, four or more. *Character 53.* Trichobothria femur III: 0, absent; 1, present (Fig. 46*H*).

Character 54. Trichobothria femur IV: 0, absent; 1, present.

Character 55. Trichobothrium metatarsus IV: 0, present; 1, absent.

Behaviour

Character 56. Web: 0, without a funnel; 1, with funnel into a retreat (Figs 6*C*, 7*D*).

Results of cladistic analysis

Hennig86, using the implicit enumeration command (exact solution), finds three cladograms of 92 steps, with consistency and retention indices of 0.73 and 0.83, respectively. The same three topologies are found using heuristic searches in NONA. The strict consensus cladogram, 95 steps, groups the four Orsonwelles species used in the analysis, but collapses the intergeneric relationships between Microlinyphia, Linyphia, Neriene and Orsonwelles. Although four taxa can theoretically produce 15 possible fully resolved topologies, only three cladograms of minimal length exist for the character data: Orsonwelles sister to Neriene plus (Linyphia + Microlinyphia); Orsonwelles sister to Microlinyphia plus (Linyphia + Neriene); or Microlinyphia sister to Orsonwelles plus (Linyphia + Neriene). Successive character weighting (Farris 1969) by the rescaled consistency index (Farris 1989) stabilises, at the second iteration, on the third topology. This topology has been adopted as a working hypothesis and used to optimise the 92 character state changes (Fig. 1).

Labulla thoracica, the type species of the genus that, until now, contained the only two named species of Orsonwelles, is only distantly related to the Hawaiian taxa. Labulla occurs at the base of the Linyphiini clade, sister to the other linyphiine taxa included in the analysis.

The monophyly of the genus Orsonwelles is well supported (BS >10). Twenty-six synapomorphies, six of them homoplasious (Fig. 1), support the monophyly of the genus Orsonwelles (only the optimisation of character 49 is ambiguous, the remaining 25 changes are unambiguous). Some of the most conspicuous synapomorphies of Orsonwelles include: the long male pedipalpal tibia; knobshaped (armless) paracymbium with a cymbial orifice; retromarginal cymbial apophysis; elongate tegulum; mesal position of tri- or tetralobed terminal apophysis; large mesal tooth of the lamella characteristica (this tooth has a basal position); absence of a dorsal plate scape in the epigynum; absence of an epigynal atrium and of a turning point in the copulatory ducts; mesal orientation of the fertilisation ducts; absence of cheliceral stridulatory striae; large number of prolateral and retrolateral cheliceral teeth; presence of trichobothria on femora III and IV; and presence of a trichobothrium on the fourth metatarsus. Additional support



Fig. 1. One of the three most parsimonious cladograms that result from the analysis of the character data given in Table 1 (Length = 92, Consistency Index = 0.73, Retention Index = 0.83). Character state changes are mapped using Farris optimisation; homoplasious changes are represented by open circles. Numbers adjacent to nodes represent Bremer support values; nodes without support values are collapsed in the strict consensus cladogram (see text for details).

The four species of *Orsonwelles* sampled in this study occur in two clades. One clade includes the two species from Kauai (*O. malus* and *O. calx*) and is sister to the clade that includes the two species from Oahu (*O. polites* and *O. arcanus*).

Discussion

Morphology

There is robust character support for the monophyly of Orsonwelles. The genus is highly unusual, exhibiting some features that have never been described in the Linyphiidae. For example, all species of Orsonwelles have trichobothria on femora III and IV (Figs 46H, 48E). Femoral trichobothria are rare in the Araneoidea (Griswold et al. 1998), with the exception of some tetragnathids (Hormiga et al. 1995), and to my knowledge have never been reported in the Linyphiidae. The male palpal morphology of Orsonwelles is also very characteristic, although for the most part, the sclerites are easily hypothesised as homologous with those of other linyphiines. The overall palpal morphology resembles, to some extent, that of Neriene, although it differs significantly in detail. This similarity between Neriene and Orsonwelles points to a potential cladistic problem. If Orsonwelles derived from a species of Neriene that colonised the Hawaiian Islands, ranking the Hawaiian species as a genus could render Neriene paraphyletic. This is a common, and old, systematics problem caused by long branches (e.g. the classic case of birds and the paraphyly of Reptilia). Thus the question to be posed when ranking island taxa grouped by a very long branch is whether a paraphyletic group is being simultaneously created. To address this potential problem, I included two species of Neriene in the character matrix. In none of the three minimum length topologies does Orsonwelles appear as sister to Neriene. In fact, none of the three cladograms supports any single genus as the sister group of Orsonwelles. This result is not surprising given the absence of a hypothesis of sister-group relationship for Orsonwelles. It is possible that the long branch length of Orsonwelles is, in part, artifactual and could be 'shortened' by adding a closer outgroup.

Spinneret morphology is quite uniform in *Orsonwelles*, and fairly similar to that of other linyphilds (Hormiga 1994*b*, 2000). I have found only minor differences in the number of spigots of *Orsonwelles* species, particularly aciniform gland spigots, and although this variation could be phylogenetically informative, an assessment of the intraspecific variation is required before it can be coded as a cladistic character. Adult males of *Orsonwelles malus* are unique among the members of this new genus in that they retain the PLS triad (Fig. 38*B*; this has been confirmed by

examining four males of this species). The triad is usually reduced to nubbins in adult non-erigonine linyphiid males (Fig. 39*F*). In the past, on the discovery of the retention of the male triad in adult erigonines (Hormiga 2000), I had hypothesised that this retention could be a case of progenesis, that is, precocious sexual maturation of juvenile males, based on the fact that the male araneoids that had the triad are usually small-sized (e.g. cyatholipids, Griswold 2001). The case of *O. malus*, a large spider, does not fit this general trend.

Very little is known about the epiandrous fusules of linyphiids (e.g. Fig. 58B). These silk organs are found on the male epigastric furrow and are allegedly used to produce the silk needed to build the sperm web prior to induction (Marples 1967; Melchers 1964). These fusules were first discovered by Machado in the Ochyroceratidae (Fage and Machado 1951; Machado 1951). Marples (1967: 221) reported the presence of epiandrous fusules in members of more than a dozen spider families (although no linyphiid species were included in her survey) and noted that in some taxa, the fusules are grouped and located in cuticular pits. Marples (op. cit., p. 221) also reported intraspecific variation for the araneid, Eriophora pustulosa (Walckenaer) (cited as A. pustulus), 'one individual had 17 pits, while two others had seven and nine larger ones'. Peters and Kovoor (1991, figs 10 and 11) described these male epigastric spigots and its silk glands in Linyphia triangularis (Clerck), reporting that the fusules were single or in groups of two to four, coming out from roundish depressions. I have examined the epiandrous fusules in the eight Orsonwelles species for which I had sufficient specimens for SEM study (Figs 38D, 40B, 44G, 48B, 52B, 54B, 56B, 58B), but I have not studied its morphological intraspecific variation, which is imperative to assess its phylogenetic information content. The number of fusules ranges from 14 (O. graphicus) to 33 (O. ambersonorum), with most species having around 20. The fusules, shorter but similar in diameter to the macrosetae of the epigastric region, are roughly equally spaced and arranged more or less in a row along the margin of the furrow. Sometimes two shafts share a common base. This pattern contrasts with the condition in other linyphiines (listed in Appendix 1). In Bolyphantes luteolus (Blackwall), Labulla thoracica, Pityohyphantes costatus (Hentz), Linyphia triangularis, Neriene radiata (Walckenaer) and Microlinyphia dana (Chamberlin and Ivie) the fusules are found in pits and are clustered in groups of two to seven. Mynoglenine linyphiids (Afroneta sp., Haplinis diloris (Urquhart) and Novafroneta vulgaris (Blest)) have about a dozen fusules arranged in a row, more or less equally spaced. In the six erigonine species that I have examined (Ceratinops inflatus (Emerton), Dismodicus decemoculatus Emerton, Erigone psychrophila (Thorell), Laminacauda plagiata (Tullgren), Sciastes truncatus (Emerton) and Typhochrestus digitatus (O. P.- Cambridge)) the fusules are absent. The

absence of epiandrous fusules should be interpreted as apomorphic for this linyphiid subfamily, although more taxa need to be studied to corroborate this putative synapomorphy of Erigoninae. Interestingly, Nielsen (1932: 209) seems to suggest that *Erigone arctica* (White) does not make a sperm web, which would be congruent with the lack of epiandrous fusules in erigonines. Within the family Pimoidae, the sistergroup of Linyphiidae (Hormiga 1993), the arrangement varies from singles (*Pimoa altioculata* (Keyserling)) to clusters of 2–3 fusules (*P. breuili* (Fage)). Although the epiandrous fusules are grouped in *P. breuili*, they do not come out from a common pit as they do in some linyphiids (this variation may be phylogenetically informative).

Insular gigantism

Perhaps the single most striking morphological feature of species of Orsonwelles is their extraordinarily large size. Some females (O. malus) reach a total length of more than 14 mm, which makes them the largest known linyphilds. Outside Orsonwelles, the largest linyphild I have been able to find is Laminacauda gigas Millidge, an erigonine from the Juan Fernández Islands in which the females can reach up to 9.9 mm total length (Millidge 1991). Blest (1979) describes the mynoglenine genus Haplinis Simon, from New Zealand, as reaching up to 10 mm, but none of his species descriptions cover an animal this large, the largest being H. titan Blest in which females reach almost 9 mm. Neither Laminacauda Millidge nor Haplinis are close relatives of Orsonwelles, since these two genera belong to different linyphild subfamilies. Other large linyphiids include Dubiaranea grandicula Millidge, from Peru, with females measuring 7.5-9.0 mm and males ranging 5-5.1 mm. Dubiaranea Mello-Leitao is the most speciose genus of Neotropical linyphiids, with about 100 species described and many more awaiting description (Hormiga, unpublished data); most of these species range in total length between 2.5 and 5 mm (Millidge 1985, 1991). Interestingly, all the Dubiaranea species longer than 6 mm (a total of five) are found in Peru and four of them live in the same area (Parque Nacional Abiseo). In the Holarctic region, the largest linyphilds seem to be the European species Linyphia tenuipalpis Simon, in which females reach 7.5 mm, and the Western North American species Neriene litigiosa (Keyserling), with females up to 8.5 mm (van Helsdingen 1969). Thus, given this gap in body size between the largest linyphines and species of Orsonwelles, the large size of Orsonwelles is hypothesised to be synapomorphic, providing additional evidence for the monophyly of the genus.

Gigantism is common in insular taxa (Carlquist 1974; Whittaker 1998), including several invertebrate groups in the Hawaiian Islands, such as some amastrid snails, dragonflies of the genus *Anax* Leach and the grasshopper *Banza nihoa* Hebard (Carlquist 1980). In spiders, insular gigantism has been noted by Berland (1924) for several species from Juan Fernández Islands. Berland cites, among others, the case of the large linyphiid Leptorhoptrum platei (F. O. P.-Cambridge). Leptorhoptrum platei is most likely a senior synonym of the aforementioned Laminacauda gigas. Millidge (1991), unaware of the works of Cambridge (1899) and Berland (1924), described several new species from Juan Fernández, and in doing so he must undoubtedly have created some junior synonyms. The neotropical erigonine genus Laminacauda contains 35 species, 24 of them are continental and are distributed between Panama and southern Chile (some of those species are also found in the Galapagos and Falkland islands). In addition, the Juan Fernández and Tristan da Cunha islands have seven and four endemic species, respectively, and of those, two in the former (three if Leptorhoptrum platei is not a junior synonym) and one in the latter are gigantic relative to the mainland species. I have examined paratype specimens of L. gigas, and in addition to being one of the largest known linyphiids, it has some striking similarities with Orsonwelles: the chelicerae are massive and have a long row of large cheliceral teeth (11 anterior in both sexes and 9 and 11 posterior in the female and male respectively). This is a remarkable case of morphological convergence among very distantly related linyphiids from two groups of Pacific volcanic islands exhibiting features that are found nowhere else in the family: the extremely large body size; and a long row of numerous large cheliceral teeth. Additional cases of spider insular gigantism have been described by Bristowe (1963, 1969: 118) for the wolf spiders Hogna ingens (Blackwall) and H. maderiana (Walckenaer) (Lycosidae) from Madeira and by Arnedo and Ribera (1997, 1999) for several Dysdera species (Dysderidae) from the Canary Islands.

Web architecture

All the species of Orsonwelles studied have very similar web architecture (see 'Natural history' section under the genus description), and with a few exceptions, their webs are built on similar substrates. Unfortunately, there is remarkably little data published about the web architecture of the Linyphiidae. Most of the data consists of photographs and/or cursory descriptions in books for general audiences that focus on the largest and most common species (e.g. Emerton 1902; Nielsen 1932; Comstock 1940; Shinkai and Takano 1984). Orsonwelles web architecture is similar to that of some Neriene species (e.g. N. helsdingeni (Locket) or N. variabilis (Banks), Hormiga, unpublished data), except for the funnel, which is exclusive to the former genus, and the substantial web size differences. The webs of some species of the neotropical genus Dubiaranea also resemble that of Orsonwelles (Hormiga, unpublished data). Labulla thoracica webs differ in having very few, if any, lines over the main sheet (Nielsen 1932; Hormiga, unpublished data). It seems generally accepted that often, but not always, closely related spider species build similar webs (Eberhard 1990,



Fig. 2. Orsonwelles polites, sp. nov. from the Waianae Range of Oahu.

and references therein), and in this sense it is not surprising that Orsonwelles species have very similar architecture. However, I believe that this is the first time that the web architecture of all species (with the exception of the presumably extinct O. torosus) of a relatively large clade of araneoid spiders is examined. Eberhard (1990) has documented how within orbicularians some apparently basic web characters are not constant within the genus. Thus, it is important not to assume the uniformity of web architecture among closely related species. A good example is provided by the linyphiid genus Tapinopa Westring. While the Palearctic and North American species, T. longidens (Wider) and T. bilineata Banks respectively, are morphologically very similar (Thaler 1983; Saaristo 1996), their webs are not. The web of T. longidens is a dense sheet built across small depressions or on mosses in the ground, this web has a glittering appearance, looking as if it were covered with slime (Nielsen 1932; Toft 1980; Hormiga, unpublished data). The web of T. bilineata is built against a surface, such as a tree trunk, and consists of two small horizontal sheets of approximately the same size, in parallel, stitched around its perimeter (Hormiga, unpublished data). Both web architectures are unusual within the context of linyphiid web architecture and very different from each other (the webs of Mecynidis spp. are somewhat similar, but they are built between two parallel leaves and the sheets are not stitched around their perimeter (Scharff 1990; Hormiga, unpublished data)).

Biogeography

All Orsonwelles species are single island endemics. They have very narrow geographic distribution ranges, with the exception of O. polites (Waianae Mts, Oahu), O. falstaffius (East and West Maui) and O. graphicus (Hawaii). This pattern is common in many Hawaiian terrestrial arthropods, e.g. the endemic cricket genus Laupala Otte (Shaw 1996a). Sympatry occurs very rarely in Orsonwelles, with only one well-documented case (that of O. calx and O. ventus in the Makaleha Mts of Kauai). Compared with some of the large radiations of Hawaiian terrestrial arthropods, such as Hawaiian Drosophila flies or Tetragnatha spiders, the radiation of Orsonwelles has resulted in a relatively small number of species. Island age, rather than surface area, seems to be one of the major determinants of Orsonwelles species richness. The older the island, the more species it harbours. Kauai, the oldest island (more than five million years old), has six species and Hawaii, the youngest (about half a million years old), has one species. The monophyletic origin of Orsonwelles implies that its species diversity is the result of a single colonisation event of the Hawaiian Islands. The geographic origin of the ancestral colonising species remains a mystery whose resolution is hampered by our poor taxonomic understanding of the circumpacific linyphiid faunas. The species-level biogeographic analysis will be discussed elsewhere, but suffice to say here that the species cladistic pattern, based on combined morphological and



Fig. 3. *A*, *Orsonwelles malus*, sp. nov. δ from Kauai; *B*, same, \mathfrak{P} ; *C*, *O*. *calx*, sp. nov. \mathfrak{P} from Kauai; *D*, *O*. *ventus*, sp. nov. δ from Kauai; *E*, *O*. *ambersonorum*, sp. nov. δ from Oahu; *F*, same, \mathfrak{P} .

molecular evidence, is consistent with colonisation of the archipelago through island progression (Hormiga *et al.* in press).

Spiders are famous for their ballooning and dispersal abilities (Bristowe 1958; Foelix 1996), and among them linyphiids have often been cited as travelling long distances or colonising areas such as islands and mountaintops. For example, Bristowe (1931) describes how after the formation of the island of Anak Krakatau by eruption of a submarine volcano in 1929, spiders were among the first colonizers recorded, and among them, the linyphiid *Maso krakatauensis* Bristowe. The small size of linyphiids probably plays an important role in their dispersal abilities. The difference in size between *Orsonwelles* and the remaining members of the

Linyphiidae suggests that the process leading to the apomorphic increase in body size started after the colonisation of the Hawaiian Islands (either in one of the current Hawaiian Islands or on some intermediate island). That is, the ancestral colonising species was smaller. Nevertheless, dispersal and colonisation of Hawaii need not have occurred by means of ballooning. Rafting on drifting trees or mats of vegetation are possible alternatives (Carlquist 1980). Evidently, the presence of *Orsonwelles* in all the high islands suggests that these spiders can, and do, disperse across the sea. This fact, however, leads to a paradox. Why are all *Orsonwelles* species single island endemics? They have colonised every high Hawaiian island, so why are none of the species found on more than one island? The dispersal mechanisms, whatever they might be, are there, as evidenced by the presence of these spiders throughout the archipelago. Most of the species live in similar habitats, and some even seem capable of coping with substantial habitat degradation (e.g. those living in eucalypt forest stands). Their morphology is very similar (except for the genitalic differences), their webs are quite uniform and they are generalist predators. All these characteristics suggest that it would be logical to find at least some species of Orsonwelles on more than one island, but such is not the case. A similar pattern is found in some afromontane linyphiids of eastern Africa, with levels of endemism of 80% and higher for individual mountains, suggesting that intermontane dispersal is rare or non-existent (Scharff 1992, 1993). Island taxa often have apomorphically decreased dispersal secondarily abilities (e.g. apterous or brachypterous insects in islands). Perhaps Orsonwelles species have reduced ballooning capabilities, to the extent that dispersal, although rare, happens often enough to colonise all the islands at least once, yet remains rare enough that islands are colonised only once (M. Arnedo, personal communication). Their adult spinneret morphology is typical and shows no pattern of reduction, although I have not examined the juvenile morphology. It seems unlikely that major ampullate silk glands in juveniles, which would produce the long silk lines needed for ballooning, are reduced because these are the glands also used to produce the dragline (the spider's 'safety line') and would be under strong selective pressure. Spiders of Orsonwelles often 'drop dead' from their webs when threatened and stay immobile on the ground for some time (Fig. 4F). Although when they 'drop dead' they do not seem to leave a dragline behind, they do leave it when walk around on substrates.

Conservation

Some of the features that have made the Hawaiian archipelago a hot bed of speciation (isolation, dissected topography, diversity of habitats etc.) are also making Hawaii a hot bed of extinction. The introduction of alien species is perhaps the single and most conspicuous source of trouble for native ecosystems and indigenous biota. More than 4000 alien species have already been documented in Hawaii (Gillespie et al. 1998 and references therein). The disturbance processes (loss of habitat, arrival of invasive species etc.) started with the Polynesian colonisation of the islands and was dramatically accelerated by the arrival and settlement of Europeans. Now, plantations, pastures or urban developments occupy most of the surface area of the islands. As a consequence, a large fraction of the native biota is restricted to small and isolated areas. This pattern is especially true for many invertebrate species that are endemic to a particular mountaintop or valley. Extinctions, although documented for a few groups (e.g. Freed et al. 1987 for birds), are very poorly understood for many taxa,

including arthropods. This is in part because of our fragmentary knowledge of the biodiversity of Hawaii. Liebherr and Polhemus (1997b) have used museum collections for long-term ecological monitoring of Hawaiian species. Studying the damselflies and carabid beetles collected by R. C. L. Perkins at the turn of the nineteenth century (references in Liebherr and Polhemus 1997a), against more recent museum specimens, they were able to assess the impact of one century of alteration and transformation of the Hawaiian landscape. Although for some species Liebherr and Polhemus document large and stable populations (e.g. some coenagrionid damselflies in Molokai), others are endangered or extinct. The carabid Colpocaccus tantalus (Blackburn) belongs to the latter category. This beetle was common in Oahu in the 1890s and accounted for 39% of the carabid specimens collected by Perkins. The last specimens of this species were collected more than sixty years ago, despite intensive insect collections over the last decades. Most likely Pheidole Westwood ants played a major role in the extinction of this low elevation carabid beetle. Perkins (1913) blamed the extinction of most of the lowland arthropods on a single ant species, Pheidole megacephala (Fabricius). More recent research (e.g. Cole et al. 1992; Gillespie and Reimer 1993) has documented in detail the tremendous negative impact of ants on the native arthropods.

The small geographic distribution ranges of many Orsonwelles species, particularly those from Kauai, make these spiders particularly susceptible to environmental disturbances. As I have already mentioned, O. torosus has not been reported since Perkins collected the only known specimen at the turn of the nineteenth century. As far as I can determine, O. torosus is now extinct. Orsonwelles iudicius is only known from the summit of Haupu; given the level of endemism of Kauai and the isolated nature of this range, it seems safe to hypothesise that this species does not occur anywhere other than the higher elevations of Haupu. While it seems unquestionable that with the loss of native habitat Hawaiian indigenous species are disappearing at accelerated rates, only a few Hawaiian arthropods have been listed as endangered under the U.S. Endangered Species Act (the Kauai cave lycosid spider, Adelocosa anops Gertsch and Blackburn's sphinx moth Manduca blackburni (Butler), now known only from Maui). Gillespie et al. (1998) appropriately blame this inconsistency on the fragmentary knowledge of Hawaiian arthropods. Sound and solid monographic work provides the foundation of any biological research, including conservation biology. It is hoped that this revision provides a starting point for further research on these remarkable spiders, including how to conserve them and the unique ecosystems where they live. While this research has answered some old questions, it has also introduced numerous novel questions and exposed new gaps in our knowledge.



Fig. 4. *A*, *Orsonwelles othello*, sp. nov. δ from Molokai; B, same, \mathfrak{P} ; *C*, *O. graphicus* (Simon), \mathfrak{P} from Hawaii; *D*, *O. arcanus*, sp. nov. δ from Oahu; *E*, *O. macbeth*, sp. nov. from Molokai; *F*, *O. falstaffius*, sp. nov. \mathfrak{P} from East Maui in 'drop dead' posture.

Taxonony

Family LINYPHIIDAE Blackwall, 1859

Genus Orsonwelles, gen. nov.

Type species, Orsonwelles polites, sp. nov.

Diagnosis

Orsonwelles species can be distinguished from other linyphilds by their very large body size (total length 6.20–14.07, Fig. 4*E*) and the presence of femoral (III–IV)

trichobothria (Fig. 48*E*; no other linyphiid genus has been described to have femoral trichobothria). Chelicerae large and massive, with numerous prolateral (17–9) and retrolateral (13–7) teeth linearly arranged (Fig. 26*F*–*I*); stridulatory striae absent. Cymbium with retromarginal apophysis (Fig. 23*A*). Paracymbium a small L-shaped structure (in dorsoectal view), continuous at both ends with ectal margin of cymbium, and lacking free arm (Figs 23*B*, 43*E*). Conspicuous cymbial orifice, adjacent to paracymbium (Fig. 43*E*). Nocturnal, animals out in web only at nighttime. Sheet web (Figs 6–10) with well-defined funnel at edge of platform leading into retreat (Fig. 7*D*).



Fig. 5. *A*, *Orsonwelles falstaffius*, sp. nov. \eth from East Maui; *B*, *O. falstaffius*, sp. nov. \eth from West Maui; *C*, *O. falstaffius*, sp. nov. \clubsuit from West Maui; *D*, *O. polites*, sp. nov. \clubsuit from Oahu; *E*, same, \eth ; *F*, same, \eth moulting.

Description

Large to very large linyphild spiders, total length 6.20–11.35 in males and 8.06–14.07 in females. Carapace longer than wide, 3.27–5.70 long in males and 3.72–6.63 in females;

dark brown/grey with a light medial longitudinal band. Sternum longer than wide and prolonged between coxae IV, brownish, darker at the margins. All eyes of roughly same diameter; ALE and PLE juxtaposed. Secondary eyes with



Fig. 6. Orsonwelles webs. A, O. malus (\mathcal{Q}) , from the Waialae cabin area (Kauai); note funnel into retreat (lower right corner); B, O. malus (juvenile) from Kokee State Park (Kauai); C, O. malus (\mathcal{Q}) from Kokee State Park; note funnel into retreat (lower left corner); D, O. macbeth (\mathcal{Q}) from Pelekunu lookout (Molokai); E, O. macbeth (\mathcal{Q}) from Kamakou Preserve (Molokai); F, O. macbeth (\mathcal{Q}) from Kamakou Preserve (funnel into retreat is in upper part of web).

canoe tapetum (Figs 14F-L). PME with rhabdoms arranged in loops, positioned toward the median (Fig. 14F, I, J) (observed in *O. polites* and *O. ambresonorum*). Clypeus

height 2.02–3.26 \times one AME diameter (except in *O. graphicus*, which is *c.* 1.80). Chelicerae large and massive, slightly more divergent in males than females



Fig. 7. Orsonwelles polites webs. A, \Im from Waianae Kai (Oahu); funnel is on the right, partially shaded; B, juvenile web at Honouliuli Forest Reserve (Oahu); note abandoned old sheet at the bottom; C, \Im from Mount Kaala Natural Area Reserve; D, same web, detail of funnel; E, \Im from Palikea.

(Figs 26*F*–*I*, 46*A*–*B*) and usually darker than rest of body. Numerous cheliceral teeth (17–9 prolateral and 13–7 retrolateral), linearly arranged; prolateral teeth larger and longer than retrolateral teeth. Cheliceral stridulatory striae absent (Fig. 46*B*, *F*). Legs longer and slender in the adult male, covered with numerous setae; femur through metatarsus usually with dark annuli. Femur I 1.47–1.70 (males) and 1.10–1.63 (females) × length of cephalothorax. In females, tibia I–IV with two dorsal spines; prolateral, retrolateral and ventral tibial spines present (with a few exceptions) and variable in number; femur I–IV with dorsal spines in variable numbers; femur I–II with prolateral spines (absent in femur II in *O. calx* and *O. arcanus*); femur III–IV without prolateral spines. Metatarsal spines present in all legs. Trichobothrium metatarsus I 0.16-025; trichobothrium metatarsus IV present (located also in distal third). Femur III with 1–4 and femur IV with 1–6 dorsoectal trichobothria located at base of article (in *O. graphicus* and *O. polites* there is one trichobothrium on femur I). Female pedipalp with tarsal claw. Leg autospasy at patella-tibia junction. Abdomen ovoid, longer than wide, dark brown/grey with lighter marks (sometimes chevron-like) and some guanine spots in its anterolateral region (Fig. 3E-F). Colulus large and fleshy, with setae.



Fig. 8. Orsonwelles webs. A, O. ambersonorum (\mathcal{Q}), from Mount Tantalus (Oahu); B, O. calx (subadult \mathcal{Q}), from Laau Ridge (Kauai); C, O. othello (\mathcal{Q}), from Kamakou Preserve (Molokai); D, same web.

Spinnerets typical of linyphilinae (Hormiga 1994*b*) (Figs 59*A*–*E*). ALS with extensive piriform field and numerous tartipores (Fig. 59*B*). PMS with 1–4 aciniform spigots between cylindrical and minor ampullate spigot (Fig. 45*E*). PLS with between 6–24 dozen aciniform spigots arranged in about three rows between the two cylindrical spigots (Fig. 45*F*); base of the peripheral cylindrical spigot larger than the base of the distal one (Figs 45*E*, 59*E*). Flagelliform and aggregate spigots (araneoid 'triplet') are well developed, absent in the adult males (Fig. 39*F*), except in *O. malus*, which retain the triplet (Fig. 38*B*). Epiandrous fusules (Fig. 40*A*) arranged linearly along the posterior margin of the epigastric furrow. Fusules with long shaft, somewhat shorter than surrounding macrosetae, and more or less evenly spaced and linearly arranged.

Tracheal system (per dissection of *O. polites*) haplotracheate, with four trunks confined to the abdomen. Lateral trunks longer than median, and about twice its diameter.

Male pedipalpal tibia longer than wide, with 2-4 prolateral and 3-5 retrolateral trichobothria (Fig. 23G). Cymbial apex blunt (Fig. 23C). Paracymbium a small Lshaped structure (in dorsoectal view) continuous at both ends with the ectal margin of the cymbium and lacking a free arm; slightly less sclerotised where it connects to the cymbium (Fig. 23B). A conspicuous and deep orifice can be seen between the concave side of the paracymbium and the cymbial margin (Fig. 41F). Paracymbial apophyses absent. A more or less pointed retromarginal cymbial apophysis distad of paracymbium (Fig. 23B). Tegulum apex elongated and projected to various degrees. Suprategulum large, long (at least two thirds of the cymbium length) and narrow. Suprategular base enlarged, without a depression. Distal suprategular apophysis unciform, visible at apex of the palp (Fig. 23D). Column located at base of suprategulum in area where suprategulum connects to tegulum (Figs 23E-F). Embolus base broad (Fig. 23F); embolus long and generally not filiform in its distal half (filiform in O. falstaffius,



Fig. 9. Orsonwelles falstaffius webs. A, \Im from Waikamoi Preserve (East Maui); B, subadult \Im from Waikamoi Preserve; C, juvenile from Waikamoi Preserve; detail of repair work in main platform; D, same web, more details of repair work; E, web from mid elevations of Puu Kukui (West Maui).

O. othello and O. macbeth). Embolic membrane plumose (covered with 'papillae,' Fig. 50E). Terminal apophysis mesal, more or less tri- or tetralobed and not coiled, as wide as long or wider (Fig. 23C, E). 'Terminal sclerite' located in membranous region between radix and lamella, continuous with base of apical apophysis of lamella (Fig. 23B, F); varying in shape and appearance from large, globular and relatively sclerotised (e.g. O. othello, Fig. 51E) to small and membranous (e.g. O. malus, Fig. 37D). Lamella characteristica large (about the same length than the cymbium) and highly sclerotised, with large mesal tooth in basal position and apical apophysis (Fig. 23A, C, E). Epigynum of variable morphology, longer than wide (in ventral view) in most species from Kauai (Fig. 16A) and as wide as long, or wider, in the remaining species (Fig. 24A). Epigynal scape absent; a vestigial epigynal socket is present in the species from Kauai (Figs 38F, 40E) but absent in the remaining species. Small and globular spermathecae (Figs 24E-F, 32C-D). Copulatory ducts, of varying length,

separate from fertilisation ducts (Fig. 36E); copulatory duct turning point absent. Fertilisation ducts mesally oriented (Figs 24E-F). No evidence of an epigynal atrium.

Composition

The thirteen known species are treated in this monograph arranged by their island of origin, and the islands are dealt with in chronological order, starting by the oldest (Kauai): *O. torosus* (Simon), comb. nov.; *O. malus*, sp. nov.; *O. calx*, sp. nov.; *O. ventus*, sp. nov.; *O. bellum*, sp. nov.; *O. iudicium*, sp. nov.; *O. polites*, sp. nov. (the type species); *O. ambersonorum*, sp. nov.; *O. arcanus*, sp. nov.; *O. othello*, sp. nov.; *O. macbeth*, sp. nov.; *O. falstaffius*, sp. nov.; and *O. graphicus* (Simon), comb. nov.

Phylogenetics

The monophyly of the genus is supported by at least twentyfive morphological synapomorphies (see 'Cladistic analysis' section), the close relatives of this radiation are unknown.



Fig. 10. Orsonwelles graphicus webs in Hawaii. A, \Im from Kahaualea Natural Area Reserve; B, \Im from Puu Makaala Natural Area Reserve; C, \Im from Puu Makaala Natural Area Reserve; D, E, same web.

Natural history

Orsonwelles species are largely confined to remnants of Hawaiian native rain and mixed mesic forests (see Sohmer and Gustafson (1987) for descriptions of these vegetation zones), often at high elevation, although a few species (e.g. *O. polites*) can be found in disturbed habitats (that is, with numerous introduced plant species) at lower elevations (e.g. *O. ambersonorum* in Mount Tantalus, in the outskirts of Honolulu at *c*. 500 m of elevation). These animals are nocturnal, and very rarely can be seen outside their retreats during the day. At night they are usually found, upside-down, at the centre of their webs (Fig. 2). They are generalist predators and feed on a variety of arthropods (including amphipods in *O. macbeth*), moths are often found among their prey items.

Web architecture (Figs 6–10) is similar to that of some *Neriene* species and other linyphines, consisting of a more or less flat sheet with a dense upper mesh of silk lines, often with a simple tri-dimensional mesh under the main platform.

The main platform can vary in shape (probably as a result of the availability of attachment points), but it is often longer than wide, with the end close to the substrate narrowing into a well-differentiated funnel that goes into a retreat. This funnel has been observed in all species (Fig. 7C-D), although it is sometimes absent in the webs of early instars. The webs seem to be maintained for considerable periods of time and extensive repair, such as stitching of holes in the main platform (Fig. 9C-D), is often obvious. Repair work is done at night. Sometimes new webs are built directly above the older one (presumably by the same individual), in such a way that the remains of the older web can be seen under the main platform (Fig. 7B). The main platform seems to contain viscid sticky silk that attaches to smooth objects when touched. This conjecture is also consistent with the presence of the PLS triplet in these species. The webs function, at least at times, as malaise traps; flying insects, such as moths, are intercepted by the dense mesh of guy lines and fall down onto the main platform where the spider catches it through the silk sheet. Argyrodes spp. (Theridiidae) kleptoparasites



Fig. 11. Habitats of *Orsonwelles* species. *A*, Makaleha Mountains, seen from the Power line Trail (Kauai); *B*, Wekiu area of the Makaleha Mountains, habitat of *O. calx*, sp. nov. and *O. ventus*, sp. nov.; *C*, Haupu (Kauai); *D*, summit area of Haupu, habitat of *O. iudicium*, sp. nov.; *E*, Laau Ridge (Kauai), habitat of *O. calx*, sp. nov. (photo by I. Agnarsson); *F*, Waianae Kai, one of the localites *O. polites*, sp. nov. in the Wai'anae Range of Oahu.

are commonly found on *Orsonwelles* webs, sometimes in high numbers (23 individuals of at least two species on a *O. malus* web is the largest number I have recorded).

Orsonwelles webs are often spatially clustered, some patches of habitat will have numerous animals while others seem devoid of them. Isolated webs are rarely found.

Mating is in Type 2 position (Foelix 1996 and references therein), as typical in the Linyphildae (observed in *O. ambersonorum*). I was able to observe part of the mating courtship of *O. polites* (at Honouliuli Forest Reserve, Oahu). The male approached the female in her web, tapping the main sheet with his abdomen. Once he was in reaching distance, the male 'touched' the female with his legs, at this

point the headlamp light disrupted the mating and both animals ran away. It is common to find a male and a female sharing the web.

Etymology

This genus is named after filmmaker and actor Orson Welles (1915–1985). *Orsonwelles* is an undeclinable proper name and masculine in gender.

Distribution

All the species are single island endemics in the Hawaiian Islands (Fig. 13). Geographic distribution ranges are narrow, with the exception of *O. polites* in the Waianae Mts of Oahu,



Fig. 12. Habitats of *Orsonwelles* species. *A*, Haupu (Kauai), its summit area is the only known locality of *O. iudicium*, sp. nov.; *B*, Mount Kahili (Kauai) seen from lower elevation; *C*, Mount Kahili, habitat of *O. bellum*, sp. nov.; *D*, a native rainforest in the mid elevations of Puu Kukui (875 m) with a web of *O. falstaffius*, sp. nov.; *E*, Pihea trail, in the Alakai Swamp area of Kauai, where *O. malus*, sp. nov. can be found; *F*, the forest around the Kolekole Cabin in the Kamakou Preserve (Molokai), the type locality of *O. macbeth*, sp. nov.

O. falstaffius in East and West Maui, and *O. graphicus* on Hawaii. On the islands with more than one species of *Orsonwelles*, allopatric distribution patterns seem to be the rule, with the exception of *O. calx* and *O. ventus* in the Makaleha Mountains of Kauai and perhaps *O. othello* and *O. macbeth* on Molokai (see comments under the descriptions of the aforementioned species).

Key to the species of the genus Orsonwelles

1.	Males
2.	Terminal apophysis large (at least 2/3 size of lamella
	characteristica, Fig. 21 <i>D</i>)
	Terminal apophysis smaller (Fig. 23 <i>C</i>)

3.	Mesal cymbial apophysis present (Figs 15 <i>C</i> , 19 <i>C</i>)4
	Mesal cymbial apophysis absent5
4.	12 prolateral cheliceral teeth, eight retrolateral teeth; basal part
	of terminal apophysis divided (Fig. 15C) O. malus, sp. nov.
	18 or more prolateral cheliceral teeth, 11 or more retrolateral
	teeth; basal part of terminal apophysis undivided and twisted
	(Fig. 19 <i>C</i>) <i>O. ventus</i> , sp. nov.
5.	Ten or more prolateral cheliceral teeth, nine retrolateral teeth;
	terminal apophysis as in Fig. 17D O. calx, sp. nov.
	15 or more prolateral cheliceral teeth, ten or more retrolateral
	teeth; terminal apophysis as in Fig. 21D O. iudicium, sp. nov.
6.	12–14 prolateral cheliceral teeth7
	9–11 prolateral cheliceral teeth
7.	8-9 retrolateral cheliceral teeth; terminal apophysis as in
	Fig. 27 <i>C</i>
	Ten or more retrolateral cheliceral teeth; terminal apophysis as
	in Fig. 25D O. ambersonorum, sp. nov.



Fig. 13. Geographic distribution of Orsonwelles species.

8. Ten or more retrolateral cheliceral teeth; terminal apophysis as in Fig. 23C O. polites, sp. nov. Eight or less retrolateral cheliceral teeth; terminal apophysis Nine or less prolateral cheliceral teeth; terminal apophysis as in 9. Ten or more prolateral cheliceral teeth; terminal apophysis 10. Mesal outline of terminal apophyses smoothly curved Mesal outline of terminal apophyses barely curved (Figs 31C, 11. Terminal apophysis as in Fig. 33C, E....O. falstaffius, sp. nov. Dorsal plate of epigynum with small socket in caudal region 12. 13. Epigynum (in ventral view) at least as wide as long (Fig. 14C). Epigynum longer than wide in ventral view......14 14. 12 or less prolateral cheliceral teeth, 7-8 retrolateral teeth; epigynum as in Fig. 16A-C. O. malus, sp. nov.

15.	13–14 prolateral cheliceral teeth; epigynum as in Fig. $18A-C$.
	<i>O. calx</i> , sp. nov.
	16 or more prolateral cheliceral teeth; epigynum otherwise16
16	Three or more trichobothria on femur III: epigynum as in
101	Fig 19E U
	$\begin{array}{c} 1 \text{ if } 1 \text{ if }$
	One or two trichobothria on femur III; epigynum otherwise 1/
17.	One or two trichobothria on femur IV; epigynum as in Fig.
	22 <i>A</i> – <i>D</i>
	Three or more trichobothria on femur IV; epigynum as in
	Fig. 20 <i>C</i> – <i>F</i>
18.	One or two trichobothria on femur IV
	Three or more trichobothria on femur IV
19.	14–15 prolateral cheliceral teeth; epigynum as in Fig. $28D-E$.
	<i>O. arcanus</i> . sp. nov.
	9–13 prolateral cheliceral teeth: enjoynum otherwise 20
20	Couldel region of opigrnum (vontrol view) not incised (Fig. 204)
20.	Caudal region of epigynum (ventral view) not incised (Fig. 30A)
	Caudal region of epigynum (ventral view) incised (Fig. 32A)
21.	Three or more trichobothria on femur IV O. graphicus
	One or two trichobothria on femur IV 22
22	Tan or more retrolateral chaliceral teeth: enjoynum as in
44.	The of more retrotated chemiceral teetin, epigyintin as in Σ^2
	Fig. 34A–F O. falstaffius, sp. nov.
	7–9 or more retrolateral cheliceral teeth

Orsonwelles torosus (Simon, 1900), comb. nov. (Figs 14A–E)

Labulla torosa Simon, 1900 (in part): 464, pl. 16, fig. 1d (female description).

Labulla torosa; Simon, 1904: 341 (erroneous geographic distribution data, see comments in 'Distribution' section).

Material examined

Lectotype (designated herein). Waimea (presumably in Kauai), 1904.x.24.119, 1 \bigcirc (BMNH). N.B. – The syntype series of *Labulla torosa* Simon contains two adults of two different species (one male and one female) and one juvenile male (deposited at BMNH, examined). It is necessary to designate a lectotype to fix the status of one of the three syntype specimens as the sole name-bearing type of *Labulla torosa*. The female (Waimea, 1904.x.24.119) is designated here as the lectotype of *Labulla torosa*. The male (1904.x.24.114) belongs to *Orsonwelles malus*; the juvenile syntype male (MOLOKAI(!): Molokai Mts 914–1219 m, 1893, Perkins) cannot be identified at the species level.

Diagnosis

A discrete medial epigynal trunk, clearly widest at the centre, combined with a continuous epigynal lip is unique to O. torosus (Fig. 14A, C).

Description

Male

Unknown.

Female (lectotype)

Cephalothorax 4.65 long, 2.91 wide, 2.85 high. Sternum 2.42 long, 1.80 wide. Abdomen 6.51 long, 4.34 wide. AME diameter 0.22. Clypeus height $2.57 \times$ one AME diameter. Chelicerae with 12–13 prolateral and 9–11 retrolateral teeth (Fig. 14*E*). Femur I 6.82 long, 1.47 × the length of cephalothorax. Femoral trichobothria (III + IV): 3 + 3-4. Metatarsus I trichobothrium 0.27. Epigynum as in Fig. 14*A*–*D*.

Natural history

Unknown.

Distribution

Orsonwelles torosus is known from a single female collected by R.C.L. Perkins in the 1890s. Perkins collected this specimen in Waimea, although his collecting label does not specify the island or collecting date ('1904.x.24.119' is probably the museum accession label). Unfortunately there are other places in the Hawaiian Islands named 'Waimea' e.g. Perkins collected at Waimea, Oahu in April 1892 (Manning 1986: 33). The presence of a male of *O. malus* (endemic to the Kokee area in Kauai) in the syntype series suggests that these two animals indeed came from Kauai. Perkins collected on Kauai in 1894, 1895 and 1896; during his 1895 fieldwork on Kauai, Perkins collected both in the Waimea and Halemanu areas (Manning 1986: 36). In the latter place I have collected *O. malus*; this is consistent with the postulated Kauai origin for the single *O. torosus* specimen. The extreme and fast degradation of the Hawaiian

ecosystems since Perkins' time (e.g. see Liebherr and Polhemus 1997a, 1997b), particularly at lower elevations (including the Waimea area and its vicinity), and the absence of additional specimens (despite my attempts to find this species) suggest that *O. torosus* may be extinct.

Orsonwelles malus, sp. nov.

(Figs 3A-B, 6A-C, 15, 16, 37, 38)

Labulla torosa Simon, 1900 (in part): 464, pl. 16, fig. 1a-c (male description).

Material examined

Holotype. Kauai, Nualolo trail, $22^{\circ}07'59.2''N$ 159°39'40.0''W, 16.viii.1995, coll. G. Hormiga & J. Coddington, *c.* 1060 m, 1 δ , moulted to adult 5.ix.1995 (USNM).

Paratype. Kauai, Nualolo trail, 13.iv.1999, coll. G. Hormiga, c. 1060 m, 1 \Im (USNM). N.B. – The syntype series of *Labulla torosa* Simon (deposited at BMNH) contains two adults of two different species (one male and one female, the latter is designated as the lectotype of *torosa*) and one juvenile male (examined). The male (1904.x.24.114) belongs to *Orsonwelles malus* (see comments under *Orsonwelles torosus*).

Additional material examined. Kauai: Nualolo trail. 22°07'59.2"N 159°39'40.0"W, 13.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 1060 m, 11 9; Nualolo trail, 14-16.viii.1995, coll. G. Hormiga & J. Coddington, c. 985-1060 m, 8 males (reared from subadults), 14 9; 27.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 1060 m, 15 ♀; Nualolo Valley, 11.viii.1953, coll. D. E. Hardy, 1 male (AMNH); Kokee State Park, Halemanu trail, 22°07'14.8"N 159°39'30.2"W, 17.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 1100 m, 2 males, 22 9; 24.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 1100 m., 10 9; Near Waialae State Cabin, 22°04'56.9"N 159°35'9.7"W, 9.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 1045 m, 7 9, 2 (males moulted to adult 6.vi.00); Mohihi-Waialae, 5.iv.1996, coll. E. van der Werf, 1262 m, 1 9 (BM); Mohihi Rd., Kohua Trail head, 28.xii.1997, coll. A. Asquith, 1 ♀ (BM); Hawai (sic.), 1904.x.24.114, 1 male (ex torosa syntype series; BMNH).

Diagnosis

Cymbium with large mesal apophysis (Fig. 15*C*, *G*). Terminal apophysis very large (as large as lamella characteristica), with two conspicuous lobes near base of the cymbium in dorsal view (Fig. 15*C*, *F*, *G*). Terminal sclerite membranous (Figs 15*F*, 37*D*). Male pedipalpal tibia with five retrolateral trichobothria (Fig. 15*H*). Epigynum enormous and of swollen appearance, with cuticle less sclerotised dorsally and laterally (Figs 16*A*–*C*, 37*E*–*F*).



Fig. 14. *A*–*E*, *Orsonwelles torosus* (Simon) \mathcal{Q} (lectotype); *F*–*G*, *O. polites*, sp. nov. \mathcal{E} ; *H*–*L*, *O. ambersonorum*, sp. nov. \mathcal{E} . *A*, epigynum, cleared, ventral; *B*, same, dorsal; *C*, epigynum, ventral; *D*, same, caudal; *E*, cheliceral teeth; *F*–*L*, eye region showing tapeta (scale bars: 0.5 mm).

Description

Male (holotype)

Total length 9.30. Cephalothorax 4.71 long, 3.22 wide, 2.91 high. Sternum 2.42 long, 1.98 wide. Abdomen 4.59 long, 3.22 wide. AME diameter 0.25. Clypeus height

 $2.80 \times$ one AME diameter. Chelicerae with 12 prolateral and eight retrolateral teeth (Fig. 14*I*–*J*). Femur I 7.13 long, $1.51 \times$ the length of cephalothorax. Femoral trichobothria (III + IV): 3-6 + 6. Metatarsus I trichobothrium 0.19. Pedipalp as in Figs 15*A*–*H*, 37*A*–*D*. Pedipalpal tibia with four prolateral and five retrolateral trichobothria.



Fig. 15. Orsonwelles malus, sp. nov. δ from Nualolo trail (Kauai). A, Palp, ectoventral; B, same, ectal; C, same, dorsal; D, ventral, embolic division removed; E, detail of distal suprategular apophysis; F-G, embolic division; H, tibial trichobothria, dorsal (scale bars: 0.5 mm, except E, 0.1 mm).

Female (paratype)

Total length 13.64. Cephalothorax 5.58 long, 3.66 wide, 3.10 high. Sternum 3.04 long, 2.17 wide. Abdomen 8.06 long, 6.07 wide. AME diameter 0.30. Clypeus height $2.91 \times$

one AME diameter. Chelicerae with 10–11 prolateral and 7–8 retrolateral teeth (Fig. 14*G*–*H*). Femur I 7.44 long, 1.33 × length of cephalothorax. Femoral trichobothria (III + IV): 3 + 4-5. Metatarsus I trichobothrium 0.19. Epigynum as in Figs 16*A*–*F*, 37*E*–*F*, 38*E*–*F*.

Variation

Male cephalothorax ranges in length from 4.71 to 5.70 (n = 5). Female cephalothorax ranges in length from 4.71 to 6.08 (n = 7). Male total length ranges from 8.74 to 10.66 (n = 5). Female total length ranges from 8.93 to 14.07 (n = 7).

Natural history

Orsonwelles malus lives in mesic (in the eastern part of their range) to wet (in the western part) forests. Some of the studied specimens were collected in highly disturbed areas, like the vicinity of Waialae Cabin, an area with large o'hia trees (Metrosideros polymorpha) and abundant undergrowth of Lantana and Rubus. The webs of O. malus have the typical architecture of the genus (Fig. 6A-C). The main sheet of one web from Nualolo trail, located about 50 cm above the ground and measuring c. 60×30 cm, was held by horizontal lines up to 80 cm long and had a mesh of guy lines c. 95 cm high. These animals are sometimes spatially clustered, e.g. in Halemanu Trail (Kokee State Park) I found O. malus to be abundant in patches of New Zealand karacanut (Corynocarpus laevigatus), an introduced species, but uncommon in other types of vegetation along the trail, such o'hia trees. Webs often have Argyrodes sp. as kleptoparasites, from one web in Nualaolo trail I collected 23 individuals of at least two species of Argyrodes.

Etymology

The species epithet, from the Latin adjective meaning 'evil,' is derived from the Orson Welles film 'Touch of Evil' (1958).

Distribution

Endemic to the Kokee, Na Pali- Kona and Alakai Swamp areas in NW Kauai. This species has been collected at elevations between 985 (Nualolo Valley) and 1263 m (Mohihi-Waialae trail).

Orsonwelles calx, sp. nov. (Figs 3*C*, 8*B*, 17, 18*A*–*D*, 39, 40)

Material examined

Holotype. Kauai, Makaleha Mts, Wekiu, 22°07'1.9"N 159°24'53.2"W, 28.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 980 m, male (USNM).

Paratypes. Kauai, Makaleha Mts, Wekiu, $22^{\circ}07'1.9''N$ 159°24′53.2″W, 19–20.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, *c.* 980 m, 1 \Im ; 28.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, *c.* 980 m, 5 \Im (USNM).

Additional material examined. Kauai: Makaleha Mts, Wekiu, 22°07'1.9"N 159°24'53.2"W, 19–20.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 980 m, 7 \Im ; 28.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 980 m, 7 \Im ; Makaleha Mts, West side near Uluawaa, 3.i.1998, coll. A. Asquith, 975 m, 4 \Im ; Makaleha Mts, 1.85

km E–SE of Wekiu, Wekiu, 22°06′54.3″N 159°23′45.5″W, 25.iv.2000, coll. G. Hormiga, A. Asquith, M. Arnedo, I. Agnarsson, *c*. 705 m, 1 \Im ; Laau Ridge, N–NW of Puu Kamaha, 22°08′13.1″N 159°32′22.9″W, 4–5.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, *c*. 1225 m, 16 \Im , 4 \Im (males moulted to adult 8, 11, 12, 14.vi.2000).

Diagnosis

Terminal apophysis (Fig. 17*D*) long and laterally concave in mesal view, straight in *O. iudicium* (Fig. 21*D*) and in *O. ventus* (Fig. 19*D*). The males of *O. calx* differ from those of *O. malus* in having a smaller terminal apophysis with a single lobe near the base of the cymbium (there are two lobes in the latter species; Fig. 15*G*). Epigynum, in ventral view, an equilateral triangle with slightly concave lateral margins and the apex pointing caudally (Fig. 18*B*). In *O. iudicium* (Fig. 22*A*–*D*) the epigynum is similar but the apex is not as pointed and the lateral margins, in ventral view, are convex. The epigyna of *O. calx* and *O. iudicium* can also be distinguished when viewed laterally, in the former the dorsal surface of the epigynum is clearly exposed (Fig. 18*B*) and in the latter it is barely visible (Fig. 22*B*).

Description

Male (holotype)

Total length 6.56. Cephalothorax 3.67 long, 2.65 wide, 1.86 high. Sternum 1.95 long, 1.60 wide. Abdomen 2.96 long, 2.11 wide. AME diameter 0.20. Clypeus height 2.64 × one AME diameter. Chelicerae with 10–12 prolateral and nine retrolateral teeth (Fig. 17*F*). Femur I 5.89 long, 1.60 × length of cephalothorax. Femoral trichobothria (III + IV): 2–3 + 3. Metatarsus I trichobothrium 0.18. Pedipalp as in Figs 17*A*–*E*, 39*A*–*D*. Pedipalpal tibia with three prolateral and 3–4 retrolateral trichobothria.

Female (paratype)

Total length 10.73. Cephalothorax 4.65 long, 3.35 wide, 2.60 high. Sternum 1.92 long, 2.67 wide. Abdomen 6.51 long, 5.96 wide. AME diameter 0.26. Clypeus height $2.38 \times$ one AME diameter. Chelicerae with 13–14 prolateral and 10 retrolateral teeth (Fig. 18*D*). Femur I 6.51 long, 1.40 × the length of cephalothorax. Femoral trichobothria (III + IV): 3 + 4-5. Metatarsus I trichobothrium 0.22. Epigynum as in Figs 18*A*–*C*, 40*C*–*E*.

Variation

Male cephalothorax ranges in length from 3.67 to 5.58 (n = 4). Female cephalothorax ranges in length from 4.22 to 5.27 (n = 12). Male total length ranges from 6.56 to 10.97 (n = 4). Female total length ranges from 8.37 to 11.04 (n = 12).

Natural history

Orsonwelles calx has been found in native rainforests between 980 and 1225 m elevation. Their web architecture is



Fig. 16. Orsonwelles malus, sp. nov. from Nualolo trail (Kauai); A-H, \heartsuit ; I-K, 𝔅. A, Epigynum, lateral; B, same, ventral; C, same, caudal; D, same, cleared, ventral, E, same, detail of spermatheca and fertilisation duct; F, same, dorsal; G, cheliceral teeth; H, cephalothorax, frontal; I, cephalothorax, frontal; J, cheliceral teeth, K, tegulum with embolic division removed (scale bars: 1.0 mm, except D-F and J-K, 0.5 mm).

that typical of the genus (Fig. 8*B*); the juvenile webs seemed to have a more clearly defined mesh under the main sheet. The webs we have seen rarely had any *Argyrodes* sp.

kleptoparasites. At Wekiu (Makaleha Mts) Orsonwelles calx coexists sympatrically with O. ventus. The webs and somatic morphology of these two species seem indistinguishable in



Fig. 17. Orsonwelles calx, sp. nov. δ from Makaleha Mountains (Kauai). A, Palp, ectoventral; B, same, ectal; C, same, mesoventral; D, same, mesal; E, same, tibial trichobothria, dorsal; F, cheliceral teeth (scale bars: 0.5 mm).

the field. On our first visit to Wekiu (Fig. 11*B*), a typical native rainforest dominated by ohi'a (*Metrosideros polymorpha*) and lapalapa (*Cheirodendron platyphyllum*) trees of fairly low canopy height, we collected approximately

equal numbers of both species (not until I examined the specimens in the lab did I realise that there were two species). This situation of sympatry is unique, as far as I know, for the *Orsonwelles* radiation.

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Fig. 18. *A–D, Orsonwelles calx*, sp. nov. \mathcal{P} , from Makaleha Mountains (Kauai); *E–J, O. ventus*, sp. nov. from Makaleha Mountains. *A*, Epigynum, lateral; *B*, same, ventral; *C*, same, cleared, dorsal; *D*, cheliceral teeth; *E*, epigynum, lateral; *F*, same, ventral; *G*, same, cleared ventral, *H*, same, dorsal; *I*, cheliceral teeth, \mathcal{P} ; *J*, same, \mathcal{O} (scale bars: 0.5 mm, except *E–F*, 1.0 mm).

Etymology

This species is named after Harry Lime, Welles' character in Carol Reed's movie 'The Third Man' (1949). *Calx* is a Latin noun in apposition meaning 'lime' (that is, the mineral).

Distribution

Endemic to the Makaleha Mts and Laau Ridge (between the Wainiha and Lumahai rivers in north-central Kauai).

Orsonwelles ventus, sp. nov. (Figs 3*D*, 18*E*–*J*, 19, 41, 42*A*–*B*)

Material examined

Holotype. Kauai, Makaleha Mts, Wekiu, $22^{\circ}07'1.9''N$ 159°24′53.2W, 19–20.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 980 m, 1 & (moulted to adult, 9.v.1999; USNM).

Paratypes. Kauai, Makaleha Mts, Wekiu, $22^{\circ}07'1.9''N$ 159°24′53.2′'W, 19–20.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, *c.* 980 m, 1 \Im ; 28.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, *c.* 980 m, 2 \Im , 5 \Im (USNM).

Additional material examined. **Kauai:** Makaleha Mts, Wekiu, $22^{\circ}07'1.9''N$ 159°24'53.2''W, 19–20.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, *c.* 980 m, 6 \Im ; 28.iv.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, *c.* 980 m, 17 \Im .

Diagnosis

The presence of 18-19 prolateral cheliceral teeth in the males (Fig. 18*J*) is unique to *O. ventus* (the males of other *Orsonwelles* species have 15 or less prolateral teeth). Females can be distinguished, in ventral view, by the cordiform epigynum (Figs 18*F*, 42*A*).

Description

Male (holotype)

Total length 8.68. Cephalothorax 4.65 long, 2.98 wide, 2.17 high. Sternum 2.42 long, 1.80 wide. Abdomen 2.42 long, 1.80 wide. AME diameter 0.23. Clypeus height 2.70 × one AME diameter. Chelicerae with 18–19 prolateral and 11 retrolateral teeth (Fig. 18*J*). Femur I 6.82 long, $1.47 \times$ the length of cephalothorax. Femoral trichobothria (III + IV): 2 + 2-3. Metatarsus I trichobothrium 0.17. Pedipalp as in Figs 19*A*–*F*, 41*A*–*F*. Pedipalpal tibia with four prolateral and four retrolateral trichobothria.

Female (paratype)

Total length 10.23. Cephalothorax 4.96 long, 3.53 wide, 3.04 high. Sternum 2.85 long, 2.00 wide. Abdomen 6.14 long, 3.84 wide. AME diameter 0.30. Clypeus height 2.50 × one AME diameter. Chelicerae with 16–17 prolateral and 12–13 retrolateral teeth (Fig. 18*I*). Femur I 8.06 long, 1.63 × length of cephalothorax. Femoral trichobothria (III + IV): 3 + 3–4. Metatarsus I trichobothrium 0.17. Epigynum as in Figs 18*E*–*H*, 42*A*–*B*.

Variation

Male cephalothorax ranges in length from 4.65 to 4.96 (n = 3). Female cephalothorax ranges in length from 4.65 to 5.58 (n = 9). Male total length ranges from 8.68 to 9.30 (n = 3). Female total length ranges from 9.86 to 11.28 (n = 9).

Natural history

Orsonwelles ventus has been found in native rainforests around 980 m elevation. Their web architecture is that typical of the genus; the main sheet of a web I measured, built at the base of an ohi'a tree, was $c. 50 \times 64$ cm The webs we have seen did not have any *Argyrodes* sp. kleptoparasites. In Wekiu (Makaleha Mts) *Orsonwelles ventus* coexists sympatrically with *O. calx* (see 'Natural history' comments under the latter species).

Etymology

The species epithet, a Latin noun in apposition meaning 'wind', is derived from Welles' posthumous (and unfinished) film 'The Other Side of the Wind.'

Distribution

Known only to the Makaleha Mts in north-central Kauai.

Orsonwelles bellum, sp. nov.

(Fig. 20A–F)

Material examined

Holotype. Kauai, Mt Kahili, below radio tower, 31.viii.1997, coll. A. Asquith, 731 m, 1 ^Q (USNM).

Paratypes.~Kauai, Mt Kahili, 26.xii.1997, coll. A. Asquith, 671 m, 2 $\, \mathbb{Q}\,$ (USNM, BM).

Diagnosis

Epigynum very large, long and narrow (more than $1.5 \times$ longer than wide), running in parallel to the abdominal wall and almost reaching the spinnerets (Figs 20*C*–*D*).

Description

Male

Unknown.

Female (paratype, BM)

Total length 11.97. Cephalothorax 5.08 long, 3.16 wide, 3.10 high. Sternum 2.73 long, 2.11 wide. Abdomen 6.39 long, 5.33 wide. AME diameter 0.24. Clypeus height $3.08 \times$ one AME diameter. Chelicerae with 16 prolateral and 9–11 retrolateral teeth (Figs 20*A*–*B*). Femur I 7.44 long, 1.46 × length of cephalothorax. Femoral trichobothria (III + IV): 2 + 2-3. Metatarsus I trichobothrium 0.16. Epigynum as in Figs 20*C*–*F*.

Variation

Female cephalothorax ranges in length from 4.96 to 5.58 (n = 3). Female total length ranges from 10.54 to 11.97 (n = 3).

Natural history

I have been able to collect only four juveniles of this species at the type locality, their web architecture was that typical of the genus. Adult females have been collected in December and August; webs were found only on the windward side (A. Asquith, personal communication).

Fig. 19. Orsonwelles ventus, sp. nov. δ from Makaleha Mountains (Kauai). A, Palp, ectoventral; B, same, ectal; C, same, dorsomesal, D, same, ventral; E, G, embolic division; F, tibial trichobothria, dorsal (scale bars: 0.5 mm).

Etymology

This species, collected below the radio tower on Mount Kahili, is named after Orson Welles' 1938 radio broadcast of H. G. Wells' 'War of the Worlds.' *Bellum* (war) is a Latin noun in apposition.

Distribution

Recorded only from the mid elevations of Mt Kahili. One of the characteristics of Mt Kahili is that despite its relatively low elevation (c. 740 m just below the radio tower), it has a very wet rainforest. Ken Wood (personal communication)

Fig. 20. Orsonwelles bellum, sp. nov. \bigcirc from Mount Kahili (Kauai); *A*, Cephalothorax, frontal; *B*, cheliceral teeth; *C*, epigynum, lateral; *D*, same, ventral; *E*, same, cleared, ventral; *F*, same, dorsal (scale bars: 0.5 mm, except *A* and *C*, 0.5 mm).

reports abundant sheet webs in the area south of Kawaikini, west of the Iole stream (north of Mt Kahili), on both sides of the ridge; this ridge is continuous with Mt Kahili. It is very likely that those webs belong to *O. bellum* and that the mid elevations of Mt Kahili are the most southern point of its distribution.

Orsonwelles iudicium, sp. nov. (Figs 21, 22)

Material examined

Holotype. Kauai, Haupu, summit area, $21^{\circ}55'29.5''N$ 159°24'5.0''W, 30.iv.2000, coll. G. Hormiga & M. Arnedo, *c.* 700 m, 1 $^{\circ}$ (USNM).

Paratypes. Kauai, Haupu, summit area, $21^{\circ}55'29.5''N$ 159°24'5.0''W, 30.iv.2000, coll. G. Hormiga & M. Arnedo, *c.* 700 m, 1 δ , 2 \Im (USNM).

Diagnosis

Males of *O. iudicium* are unique in having the prolateral cheliceral teeth 2–6 clustered on a small protuberance (Fig. 21*F*–*G*). Their palp is most similar to that of *O. calx*, from which they can be distinguished by the terminal apophysis (Fig. 21*D*), long and laterally straight in dorsal view (concave in *O. calx*, Fig. 17*D*). The epigynum of *O. iudicium* is similar to that of *O. calx* but the apex is not as pointed and the lateral margins, in ventral view, are convex (Fig. 18*A*–*B*). The epigyna of *O. calx* and *O. iudicium* can also be distinguished when viewed laterally: in *O. calx* the dorsal surface of the epigynum is clearly exposed (Fig. 18*B*), whereas in *O. iudicium* it is barely visible (Fig. 22*B*).

Description

Male (holotype)

Total length 7.37. Cephalothorax 3.90 long, 2.81 wide, 2.30 high. Sternum 1.72 long, 1.95 wide. Abdomen 3.55 long, 2.34 wide. AME diameter 0.23. Clypeus height $2.73 \times$ one AME diameter. Chelicerae with 15 prolateral and 10 retrolateral teeth (retrolateral teeth 2–6 clustered on a protuberance, Fig. 21*F*–*G*). Femur I 6.37 long, 1.63 × length of cephalothorax. Femoral trichobothria (III + IV): 1–2 + 2–3. Metatarsus I trichobothrium 0.17. Pedipalp as in Fig. 21*A*–*E*. Pedipalpal tibia with three prolateral and three retrolateral trichobothria.

Female (paratype)

Total length 9.55. Cephalothorax 4.49 long, 2.85 wide, 2.65 high. Sternum 2.17 long, 1.67 wide. Abdomen 5.70 long, 4.15 wide. AME diameter 0.26. Clypeus height 2.14 × one AME diameter. Chelicerae with 15–16 prolateral and 10–11 retrolateral teeth (Fig. 22*E*). Femur I 5.89 long, 1.31 × the length of cephalothorax. Femoral trichobothria (III + IV): 1 + 2. Metatarsus I trichobothrium 0.17. Epigynum as in Fig. 22*A*–*D*.

Variation

Male cephalothorax ranges in length from 3.90 to 4.01 (n = 2). Female cephalothorax ranges in length from 4.40 to 4.49 (n = 2). Male total length ranges from 7.02 to 7.37 (n = 2). Female total length ranges from 9.55 to 9.80 (n = 2).

Natural history

Orsonwelles iudicium spins its webs under 'uluhe ferns, fairly close to the ground floor. Since the webs are covered by the 'fern canopy', it is difficult to see them without disturbing the spider and partially damaging the web and it seems close to impossible to photograph an intact web. The only area where I have seen these spiders (the summit of Haupu, 700 m, Fig. 11*D*) has almost no standing live trees since most of them were destroyed by a recent hurricane. Only in *O. arcanus* I have seen an adult *Orsonwelles* species build a web under ferns.

Etymology

The species epithet, a Latin noun in apposition, is derived from the Orson Welles film 'The Trial' (1962).

Distribution

Known only from the summit area of Haupu, a small and isolated range in south-eastern Kauai.

Orsonwelles polites, sp. nov.

(Figs 2, 7*A*–*E*, 12*D*–*F*, 14*F*–*G*, 23, 24, 43–46)

Material examined

Holotype. Oahu, Waianae Mts: Waianae Kai Forest Reserve, $21^{\circ}29'24.3''N$ 158°09'26.8''W, 7.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, *c.* 530–680 m, 1 & (USNM).

Paratypes. Oahu, Waianae Mts: Waianae Kai Forest Reserve, 7.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, *c.* 530–680 m, 4 3° , 7 9° (USNM).

Additional material examined. Oahu: Waianae Mts: Waianae Kai Forest Reserve, 7.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 530-680 m, 4 9; Mt Kaala Natural Area Reserve, near access road to summit, 13.viii.1995, coll. G. Hormiga & J. Coddington, c. 515 m, 5 &, 16 9; Mt Kaala Natural Area Reserve, near access road to summit, 13.viii.1995, 11.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 550-580 m, 3 ♂, 13 ♀; Mt Kaala, 21.viii.1993, coll. L. Garcia de Mendoza, 573 m, 1 &; Waianae Mts, Peacock Flats, 23.iv.1992, coll. R. Gillespie, 579 m, 1 ♂, 1 ♀; Waianae Mts, Pahole Natural Area Reserve, 4.iv.1993, coll. R. Gillespie & G. Roderick, 579 m, 2 ♂, 2 ♀; Waianae Mts, Honouliuli For. Res., off road to Palikea, 21°24'33.1"N 158°05'55.1"W, 9.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 565 m, Eucalyptus robusta forest, 12 ♂, 27 ♀; 17.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, 5 ♂, 5 ♀; Waianae Mts, Palikea, 21°23'26.6"N 158°05'55.6"W, 9.iv.1999, coll. G. Hormiga, c. 780 m, 1 ♀; Waianae Mts, Palikea, 20.viii.1995, coll. R. Gillespie, 792 m, 1 ♂, 2 9; Waianae Mts, Honouliuli For. Res., Kaluaa Gulch, 10.x.1976, coll. F.G. Howarth, 725 m, 1 9 (BM); Waianae Mts, 1934, coll. F.X. Williams, 1 9 (HDA); S end of Waianae Mts, 25.vi.1965, coll. T. Suman, 610 m, 1 & (BM); Waianae Mts, Kamaileunu Ridge N of Puu Kawiwi, 18.x.1975, coll. F.G. Howarth & W.C. Gagne, 760 m, night on tree trunk, 2 ් (BM).

Diagnosis

Males are diagnosed by the relatively small terminal apophysis (Fig. 23C), which in dorsomesal view has the apical process hidden under the cymbium. Females are

Fig. 21. Orsonwelles iudicium, sp. nov. δ from Haupu (Kauai). A, Palp, ectoventral; B, same, ectal; C, same, mesoventral; D, same, mesal; E, same, tibial trichobothria, dorsal; F-G, cheliceral teeth (scale bars: 0.5 mm).

diagnosed by the presence of a small median indentation in the medial region of the epigynal dorsal plate (Fig. 24B). The edges of the epigynal lips are semicircular and grooved (Fig. 24A) and are broken off in some specimens.

Description

Male (holotype)

Total length 8.37. Cephalothorax 4.65 long, 2.79 wide, 2.36 high. Sternum 2.48 long, 1.98 wide. Abdomen

Fig. 22. Orsonwelles iudicium, sp. nov. \Im from Haupu (Kauai). A, Epigynum, lateral; B, same, ventral; C, same, cleared, ventral; D, same, dorsal; E, cheliceral teeth (scale bars: 1.0 mm, except C-D, 0.5 mm).

4.40 long, 2.91 wide. AME diameter 0.23. Clypeus height 2.43 × one AME diameter. Chelicerae with nine prolateral and 10–11 retrolateral teeth. Femur I 7.38 long, $1.58 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 4 + 2–3. Metatarsus I trichobothrium 0.22. Pedipalp as in Figs 23*A*–*G*, 43*A*–*E*, 44*A*–*E*. Pedipalpal tibia with three prolateral and four retrolateral trichobothria.

Female (paratype)

Total length 10.74. Cephalothorax 5.70 long, 3.78 wide, 3.41 high. Sternum 3.41 long, 2.29 wide. Abdomen 5.33 long, 3.66 wide. AME diameter 0.28. Clypeus height 2.71 × one AME diameter. Chelicerae with 10–11 prolateral and nine retrolateral teeth. Femur I 8.12 long, $1.31 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 3-4 + 4. Metatarsus I trichobothrium 0.25. Epigynum as in Figs 24*A*–*F*, 45*A*–*B*.

Variation

Male cephalothorax ranges in length from 4.09 to 5.08 (n = 7). Female cephalothorax ranges in length from 4.96 to 6.20 (n = 8). Male total length ranges from 8.31 to 9.92 (n = 7). Female total length ranges from 8.99 to 11.78 (n = 8).

Natural history

Orsonwelles polites has been collected in mesic forests ranging from 515 to 780 m in elevation. While they can be found in native habitat, they are also present in relatively disturbed areas, e.g. in the Honouliuli Forest Reserve, O. polites webs are abundant on swamp mahoganies (Eucalyptus robusta, an introduced forestry species). Their web architecture is typical of the genus (Fig. 7A-E) and often the webs have Argyrodes sp. kleptoparasites (in Waianae Kai I counted seven and eight individuals of Argyrodes in two webs). In the Honouliuli Forest Reserve the Argyrodes sp. kleptoparasites were extremely abundant and their eggsacs could easily be seen near the Orsonwelles webs (and sometimes attached to their guy lines). The web of an adult female (Palikea trail) had guy lines c. 88 cm long and a main sheet of 72×34 cm. Juvenile webs (at the lower elevations of Mt Kaala) had a clearly defined funnel into the retreat.

Etymology

The species epithet is derived from the Orson Welles film 'Citizen Kane' (1941). *Polites* (citizen) is a Greek noun in apposition.

Distribution

Endemic to the Waianae Range, in western Oahu.


Fig. 23. Orsonwelles polites, sp. nov. δ from Mount Kaala (Oahu). A, Palp, ectoventral; B, same, ectal; C, same, dorsomesal; D, same, ventral, embolic division removed; E-F, embolic division (arrow, mesal tooth of lamella characteristica); G, tibial trichobothria, dorsal (scale bars: 0.5 mm).

Orsonwelles ambersonorum, sp. nov.

(Figs 3E-F, 8A, 14H-L, 25, 26, 47-49)

Material examined

Holotype. Oahu, Koolau Range.: Mount Tantalus, 21°19'58.9"N 157°48'58.3"W, 10.viii.1995, coll. G. Hormiga, c. 530 m, 1 $\stackrel{\circ}{\sigma}$ (USNM).

Paratypes. Oahu, Mount Tantalus, 10.viii.1995, coll. G. Hormiga, c. 530 m, 1 δ , 4 \circ ; 3.iv.1999, coll. G. Hormiga, c. 530 m, 1 δ , 1 \circ (USNM).

Additional material examined. **Oahu:** Koolau Range: Mount Tantalus, 21°19′58.9″N 157°48′58.3″W, 10–11.viii.1995, coll. G. Hormiga, c. 530 m, 1 $\overset{\circ}{\sigma}$, 5 $\overset{\circ}{\varphi}$; 3.iv.1999, coll. G. Hormiga, c. 530 m, 4 $\overset{\circ}{\sigma}$, 7 $\overset{\circ}{\varphi}$; Mount Tantalus, 28.viii.1993, coll. R. Gillespie, L. Garcia de Mendoza, G. Roderick, G. Oxford, 579 m, 3 $\overset{\circ}{\sigma}$, 4 $\overset{\circ}{\varphi}$; Mount Tantalus,



Fig. 24. Orsonwelles polites, sp. nov.; A-B, E-F, I, \Im from Mount Kaala (Oahu); C-D, \Im from Peacock Flats (Oahu); H-I, \Im from A-H, \Im ; I-K, \Im from Mount Kaala. A, C, Epigynum, ventral; B, D, same, caudal; E, same, cleared, dorsal, F, same, ventral; G, cephalothorax, frontal; H-I, cheliceral teeth (scale bars: 0.5 mm, except G-I, 1.0 mm).

17.ii.1993, coll. S. Larcher & D. Polhemus, $2 \ ^{\circ}$; Mount Tantalus, Puu Ohia Trail, 25.x.1995, coll. M. R. & E. van derWerf, 549 m, $2 \ ^{\circ}$ (BM); Tantalus Trail, Bamboo forest, 14.xi.1993, coll. V. Roth, $1 \ ^{\circ}$ (BM); Tantalus Ridge, 5.v.1990, coll. V. & B. Roth, $1 \ ^{\circ}$ (BM); Mount Tantalus, 8.vii.1959, Quate, $1 \ ^{\circ}$ (BM); Upper Pauoa Valley, 11.xi.1932, 457 m, coll. F.X. Williams, $1 \ ^{\circ}$ (HDA); Halawa Ridge, 24.xi.1952, coll. C. Hoyt, $1 \ ^{\circ}$ (BM).

Diagnosis

Males are diagnosed by the terminal apophysis (Fig. 25*D*), which in dorsomesal view can be seen projecting perpendicularly to the cymbial margin. Females are diagnosed by the presence of a deep cleavage in the dorsal



Fig. 25. Orsonwelles ambersonorum, sp. nov. δ from Mount Tantalus (Oahu). *A*, Palp, ectoventral; *B*, same, dorsal; *C*, same, ectal; *D*, same, dorsomesal; *E*, same, ventral, embolic division removed; *F*–*G*, embolic division; H, tibial trichobothria, dorsal (scale bars: 0.5 mm).

plate of the epigynum, easily seen in both ventral and caudal views (Fig. 26A-B).

Description

Male (holotype)

Total length 9.80. Cephalothorax 5.29 long, 4.03 wide, 2.91 high. Sternum 2.67 long, 2.23 wide. Abdomen

4.71 long, 3.72 wide. AME diameter 0.27. Clypeus height $2.63 \times$ one AME diameter. Chelicerae with 11-12 prolateral and 10-11 retrolateral teeth. Femur I 8.06 long, $1.50 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 2-3 + 3. Metatarsus I trichobothrium 0.21. Pedipalpa as in Figs 25A-H, 47A-F. Pedipalpal tibia with 3–4 prolateral and four retrolateral trichobothria.



Fig. 26. Orsonwelles ambersonorum, sp. nov. from Mount Tantalus (Oahu); A-G, \Im ; H-I, \eth . *A*, Epigynum, ventral; *B*, same, caudal; *C*, same, cleared, ventral; *D*, same, cleared, dorsal; *E*, cephalothorax, ventral; *F*, same, frontal; *G*, cheliceral teeth; *H*, cephalothorax, frontal; *I*, cheliceral teeth (scale bars: 1.0 mm, except A-D, 0.5 mm).

Female (paratype)

Total length 11.47. Cephalothorax 6.20 long, 3.72 wide, 2.73 high. Sternum 3.10 long, 2.54 wide. Abdomen 5.39 long, 3.66 wide. AME diameter 0.26. Clypeus height $3.26 \times$

one AME diameter. Chelicerae with 10–11 prolateral and 9–9 retrolateral teeth. Femur I 8.12 long, $1.31 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 3 + 3-4. Metatarsus I trichobothrium 0.17. Epigynum as in Figs 26*A*–*D*, 49*D*–*F*.

Variation

Male cephalothorax ranges in length from 4.96 to 5.64 (n = 7). Female cephalothorax ranges in length from 5.15 to 6.63 (n = 7). Male total length ranges from 9.80 to 11.35 (n = 7). Female total length ranges from 11.16 to 13.64 (n = 7).

Natural history

Orsonwelles ambersonorum has been collected at elevations ranging from 457 to 650 m, sometimes in highly disturbed habitats (such as Mt Tantalus). The web architecture is typical of the genus (Fig. 8*A*). Webs are built fairly close to the ground and commonly have *Argyrodes* sp. kleptoparasites. On Mt Tantalus (Puu Ohia trail), I found *O. ambersonorum* to be very common, although spatially clustered. Webs were very often adjacent to each other and individuals in all developmental stages, from early juveniles to adults, were common (in April). The main sheet of one web, built by an adult female, measured 35 × 25 cm and had a funnel of *c*. 2.5 cm in diameter. Mating position is Type 2.

Etymology

The species epithet is derived from the Orson Welles film 'The Magnificent Ambersons' (1942).

Distribution

Known only from the southern end of the Koolau Range of Oahu.

Orsonwelles arcanus, sp. nov.

(Figs 4D, 27, 28, 42C-F, 50)

Material examined

Holotype. Oahu, Koolau Range, Poamoho trail, $21^{\circ}31'54.0''N$ 157°55'59.4''W, 10.iv.1999, coll. G. Hormiga, R. Gillespie, N. Scharff, M. Arnedo, 680 m, 1 δ (USNM).

Paratype. Oahu, Koolau Range, Poamoho trail, 10.iv.1999, coll. G. Hormiga, R. Gillespie, N. Scharff, M. Arnedo, 600 m, $1 \$ (USNM).

Additional material examined. **Oahu:** Koolau Range, Poamoho trail, 10.iv.1999, coll. G. Hormiga, R. Gillespie, N. Scharff, M. Arnedo, c. 650 m, 3 δ , 4 φ ; Koolau Range, Puu Kaaumakua summit area, 6–7.v.1996, coll. D. Polhemus, A. Asquith, C. Ewing, 762–817 m, beating vegetation, 1 φ .

Diagnosis

Although similar to *O. ambersonorum*, the long and thin apical apophysis of the lamella characteristica (Fig. 27A-C) is unique to *O. arcanus*; the shape of the terminal apophysis (Fig. 27C) is also diagnostic. Females can be diagnosed, in ventral view, by the partially exposed dorsal plate under the epigynal lip (Fig. 28B).

Description

Male (holotype)

Total length 8.01. Cephalothorax 4.17 long, 2.30 wide, 2.65 high. Sternum 2.16 long, 1.62 wide. Abdomen 2.16 long, 1.62 wide. AME diameter 0.21. Clypeus height 2.88 × one AME diameter. Chelicerae with 12–14 prolateral and 8–9 retrolateral teeth. Femur I 6.27 long, $1.50 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 1–2 + 2–2. Metatarsus I trichobothrium 0.17. Pedipalpa as in Figs 27*A*–*G*, 50*A*–*F*. Pedipalpal tibia with 3 prolateral and 3 retrolateral trichobothria.

Female (paratype)

Total length 9.92. Cephalothorax 4.71 long, 2.98 wide, 2.67 high. Sternum 2.23 long, 1.86 wide. Abdomen 4.84 long, 3.78 wide. AME diameter 0.31. Clypeus height 2.20 × one AME diameter. Chelicerae with 14 prolateral and 11–13 retrolateral teeth. Femur I 5.83 long, $1.24 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 1-2 + 1-2. Metatarsus I trichobothrium 0.18. Epigynum as in Figs 28*A*–*E*, 42*C*–*E*.

Variation

Male cephalothorax ranges in length from 3.72 to 4.41 (n = 4). Female cephalothorax ranges in length from 4.15 to 4.71 (n = 4). Male total length ranges from 7.80 to 8.18 (n = 3). Female total length ranges from 8.68 to 9.92 (n = 4).

Natural history

Orsonwelles arcanus has been collected in native rainforests at elevations ranging from 650 to 817 m. Webs along the Poamoho trail were built mostly under 'uluhe ferns, similar to those of *O. iudicium*.

Etymology

The species epithet, a Latin noun in apposition meaning 'hidden, concealed', is derived from the Orson Welles film 'Mr. Arkadin/Confidential Report' (1955).

Distribution

Known from only two areas in the central-western region of the Koolau Mountains of Oahu.

> *Orsonwelles othello*, sp. nov. (Figs 4*A*–*B*, 8*C*–*D*, 29, 30, 51, 52)

Material examined

Holotype. Molokai, Kamakou Preserve, intersect. Maunahui Rd./ Puu Kauwa Rd., 21°08′17.8″N 156°56′56.8″W, 25.vii.1995, coll. G. Hormiga & J. Coddington, 845 m, 1 ♂ (USNM).

Paratype. Molokai, Kamakou Preserve, intersect. Maunahui Rd./ Puu Kauwa Rd., 25.vii.1995, coll. G. Hormiga & J. Coddington, 845 m, $1 \$ (USNM).



Fig. 27. Orsonwelles arcanus, sp. nov. δ from Poamoho trail (Oahu). *A*, Palp, ectoventral; *B*, same, ectal; *C*, same, dorsomesal; *D*, same, mesoventral, embolic division removed; *E*–*F*, embolic division; *G*, tibial trichobothria, dorsal (scale bars: 0.5 mm).

Additional material examined. **Molokai:** Kamakou Preserve, Kolekole Cabin trail, 21°06′46.2″N 156°54′27.4″W, 25.vii.1995, coll. G. Hormiga & J. Coddington, 1105 m, 12 \Im ; 14.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 1080 m, 1 \Im ; Kamakou Preserve, intersect. Maunahui Rd/Puu Kauwa Rd, 25.vii.1995, coll. G. Hormiga & J. Coddington, 845 m, 2 \Im , 25 \Im ; Kamakou Preserve, Pepeopae trail, $21^{\circ}07'16.4''N$ 156°53'46.8''W, 12.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, *c*. 1260 m, 1

Diagnosis

Males are diagnosed by the terminal apophysis (Fig. 29C), which in dorsomesal view has a deep curved incision



Fig. 28. Orsonwelles arcanus, sp. nov. from Poamoho trail (Oahu); A-G, \Im ; H, \eth . A, Epigynum, lateral; B, same, ventral; C, same, caudal; D, same, cleared, ventral; E, same, dorsal; F, cephalothorax, frontal; G-H, cheliceral teeth (scale bars: 1.0 mm, except D-E and G-H, 0.5 mm).

between a pointed apical process and a blunt basal process. The morphology of the terminal apophysis in *falstaffius* (Fig. 33*C*), *O. macbeth* (Fig. 31*C*) and *O. graphicus* (Fig. 35*C*) is similar, but the incision is not as deep and marked as in *O. othello*. Females are diagnosed by the presence of a small median indentation in the medial region of the epigynal dorsal plate (Fig. 30*A*). The epigynum of *O. othello* (Fig. 30*A*–*E*) is most similar to that of *O. falstaffius* (Fig. 34*A*), *O. macbeth* (Fig. 32*A*) and

O. graphicus (Fig. 36*A*). It differs from these three latter species in having, in ventral view, the caudal epigynal margin convex, never concave.

Description

Male (holotype)

Total length 9.92. Cephalothorax 4.70 long, 3.19 wide, 2.94 high. Sternum 2.50 long, 1.91 wide. Abdomen



Fig. 29. Orsonwelles othello, sp. nov. δ from Kamakou Preserve (Molokai). *A*, Palp, ectoventral; *B*, same, ectal; *C*, same, dorsomesal; *D*, same, ventral, embolic division removed; *E*–*F*, embolic division; *G*, tibial trichobothria, dorsal (scale bars: 0.5 mm).

4.90 long, 3.28 wide. AME diameter 0.25. Clypeus height $2.53 \times$ one AME diameter. Chelicerae with 10–11 prolateral and seven retrolateral teeth. Femur I 7.44 long, $1.58 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 2 + 2. Metatarsus I trichobothrium 0.24. Pedipalp as in Figs 29*A*–*G*, 51*A*–*F*. Pedipalpal tibia with 3 prolateral and 4 retrolateral trichobothria.

Female (paratype)

Total length 11.78. Cephalothorax 5.89 long, 3.10 wide, 3.10 high. Sternum 2.91 long, 1.92 wide. Abdomen 6.82 long, 5.02 wide. AME diameter 0.25. Clypeus height 2.55 \times one AME diameter. Chelicerae with 11 prolateral and eight retrolateral teeth. Femur I 6.45 long, 1.10 \times the length

of cephalothorax. Femoral trichobothria (III + IV): 2 + 2. Metatarsus I trichobothrium 0.24. Epigynum as in Figs 30A-E, 52C-E.

Variation

Male cephalothorax ranges in length from 4.34 to 5.08 (n = 5). Female cephalothorax ranges in length from 4.09 to 5.89 (n = 4). Male total length ranges from 8.37 to 9.92 (n = 5). Female total length ranges from 9.23 to 13.14 (n = 4).

Natural history

This species has been collected in the Molokai Mountains between 845 and 1260 m of elevation. In July 1995 I found it to be very abundant (both adults, including many extremely large gravid females, and juveniles) in the area below the Kamakou Preserve, at c. 845 m, spinning their webs off the swamp mahogany (Eucalyptus robusta) trunks. In May 2000 I could not find a single individual of this species in the same area or in its vicinity (apparently it had been unusually dry during the previous months). This area was replanted with swamp mahoganies during the 1930s to reforest an area where the native forest had been cut to grow cattle pasture. Orsonwelles othello can also be found in native mesic forest along the Puu KoleKole Cabin trail (c. 1000-1100 m). A single female was also collected along the Pepeopae trail, with wetter forest and high abundance of O. macbeth. This is the only case, aside from that of O. calx and O. ventus in the Makaleha Mountains of Kauai, in which two species of Orsonwelles coexist sympatrically. However, in contrast with the case in Kauai, in which both species seemed equally abundant, in Pepeopae we collected 20 adults of O. macbeth and only a single adult of O. othello. Admittedly, sympatry between O. othello and O. macbeth is only very weakly supported (i.e. the presence of the single O. othello female collected among the populations of O. macbeth could be accidental) and more geographic areas need to be studied to better understand this pattern. It seems that O. othello occupies the more mesic habitat and is then replaced by O. macbeth in the wetter areas. The web architecture of O. othello is that typical of the genus (Figs 8C-D). An unusually long web along the Puu KoleKole Cabin trail (1160 m) was found, about 35 cm above the ground, to have a main sheet of 110×19 cm.

Etymology

The species epithet, a proper name in apposition, is derived from the Orson Welles film 'Othello' (1952).

Distribution

Endemic to the western end of the Molokai mountains.

Orsonwelles macbeth, sp. nov. (Figs 4*E*, 6*D*–*F*, 31, 32, 53, 54)

Material examined

Holotype. Molokai, nr. Kolekole Cabin, 21°06′27.2″N 156°53′49.2″W, 18–20.x.1993, coll. G. Oxford & A. Tan, *c*. 1158 m, 1 ♂ (USNM).

Paratypes. Molokai, nr. KoleKole Cabin, 18–20.x.1993, coll. G. Oxford & A. Tan, c. 1158 m, 1 $\stackrel{\circ}{\sigma}$, 7 $\stackrel{\circ}{\circ}$ (USNM).

Additional material examined. **Molokai:** Kolekole Cabin, 21°06'27.2"N 156°53'49.2"W, 12.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 1165 m, 2 \Im ; Kaunuohua, top of transect 7 trail, up from Kolekole cabin, 16.iii.1991, coll. R. Gillespie; 1158 m, 1 \Im ; Kaunuohua, 18.iii.1991, coll. R. Gillespie, 1295 m, 2 \Im ; Kamakou Preserve, Pepeopae trail, 21°07'16.4"N 156°53'46.8"W, 12.v.2000, coll. G. Hormiga, M. Arnedo, I. Agnarsson, c. 1150–1260 m, 6 \Im , 19 \Im ; Kamakou Preserve, boardwalk, 6.ix.1996, coll. M. R., B. Thorsby, 1219 m, 1 \Im ; Rainforest near Kolekole cabin, 22.x.1997, coll. D. Polhemus, pyrethrin fog of mossy ohia log on forest floor, 1189 m, 2 \Im ; Ridge camp SW of Kaunuohua, 30.v.1997, coll. D. Polhemus, ohia fog no. 10, 1 \Im ; Kamakou, Pelekunu, 18.iii.1991, coll. R. Gillespie, 1295 m, 2 \Im ; Im. Sandwich (probably Molokai), no. 8681, 1 \Im (misidentification, Simon's handwritten label reads '*Labulla torosa*', MNHN).

Diagnosis

Males are diagnosed by the terminal apophysis (Fig. 31C), which is very similar in O. macbeth, O. falstaffius, O. othello and O. graphicus, but distinguishable. The main differences are found in the form of the apical and basal processes, the shape of the curve between these two processes, and the shape of the curve between the basal and ectal process. Orsonwelles macbeth (Fig. 31E, G) has the curved incision between the apical and basal process very inconspicuous (it is much more concave in O. falstaffius, O. othello and O. graphicus). The apical process is widest in O. falstaffius (Fig. 33E). The basal process is widest in O. othello (Fig. 29E). Orsonwelles graphicus has the deepest curvature between the ectal and basal processes (Fig. 35E). Females are diagnosed by the presence of a small median indentation in the medial region of the epigynal dorsal plate (Fig. 32A-B). The epigynum of O. macbeth (Fig. 32A-B) is most similar to that of O. othello, O. falstaffius and O. graphicus. In O. othello the caudal epigynal margin is convex, whereas in O. macbeth (and falstaffius, and graphicus) it is concave (Fig. 32A). The posteriomedial region of the epigynum of O. falstaffius is much longer than that of O. macbeth or O. graphicus. In ventral view, the epigynal trunk of O. macbeth is much more marked than that of O. graphicus; also, in O. macbeth the anterior region of the medial epigynal opening is not clearly delimited (Fig. 32A-B) while in O. graphicus it is demarcated anteriorly by the continuation of the lateral margins (Fig. 36A).

Description

Male (holotype)

Total length 8.62. Cephalothorax 4.40 long, 2.54 wide, 2.48 high. Sternum 3.29 long, 2.79 wide. Abdomen



Fig. 30. Orsonwelles othello, sp. nov. from Kamakou Preserve (Molokai); A-E and $H-I \ \Im$; F-G, \Im . *A*, Epigynum, ventral; *B*, same, caudal; *C*, same, lateral; *D*, same, cleared, ventral; *E*, same, dorsal; *F*, *I*, cheliceral teeth; *G*, chelicera, frontal; *H*, cephalothorax, frontal (scale bars: 0.5 mm, except G-H, 1.0 mm).

4.34 long, 2.91 wide. AME diameter 0.20. Clypeus height $2.56 \times$ one AME diameter. Chelicerae with ten prolateral and 7–8 retrolateral teeth. Femur I 6.82 long, $1.55 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 2 + 2. Metatarsus I trichobothrium 0.16. Pedipalp as in Figs 31A-G, 53A-E. Pedipalpal tibia with three prolateral and three retrolateral trichobothria.

Female (paratype)

Total length 9.80. Cephalothorax 4.40 long, 2.79 wide, 3.10 high. Sternum 2.60 long, 1.86 wide. Abdomen 6.39 long, 1.86 wide. AME diameter 0.26. Clypeus height $2.02 \times$ one AME diameter. Chelicerae with 11 prolateral and 8–9 retrolateral teeth. Femur I 6.39 long, 1.45 × length of



Fig. 31. Orsonwelles macbeth, sp. nov. A–F, \mathcal{S} from KoleKole Cabin area (Molokai); G, \mathcal{S} from Kaunuohua (Molokai). A, Palp, ectoventral; B, same, ectal; C, G, same, dorsomesal; D–E, embolic division; F, tibial trichobothria, dorsal (scale bars: 0.5 mm).

cephalothorax. Femoral trichobothria (III + IV): 2 + 2. Metatarsus I trichobothrium 0.19. Epigynum as in Figs 32A-D, 54C-F.

Variation

Male cephalothorax ranges in length from 3.72 to 5.27 (n = 5). Female cephalothorax ranges in length from 4.84 to

5.58 (n = 6). Male total length ranges from 8.37 to 10.54 (n = 5). Female total length ranges from 9.61 to 12.65 (n = 6).

Natural history

Orsonwelles macbeth has been collected in native rainforests ranging from 1165 to 1296 m in elevation. The web



Fig. 32. Orsonwelles macbeth, sp. nov. A, C–D, F, \Im , E, \Im from KoleKole Cabin area (Molokai); B, \Im from Kaunuohua (Molokai). A–B, Epigynum, ventral; C, same, cleared, ventral; D, same, dorsal; E–F, cheliceral teeth (scale bars: 0.5 mm).

architecture is typical of the genus (Fig. 6D–F). At the Pelekunu lookout, the main sheet of one of the webs measured 55×44 cm, had a clear funnel into a retreat and was about 160 cm above ground level; another web (near Kolekole cabin) had guy lines 45 cm high and a main sheet measuring *c*. 48 × 29 cm. *Argyrodes* sp. kleptoparasites are common in their webs. In the Pepeopae area *O. macbeth* has been found feeding on the amphipods, among other things, that live on the mosses and epiphytes.

Etymology

The species epithet, a proper name in apposition, is derived from the Orson Welles film 'Macbeth' (1948).

Distribution

Endemic to the western end of the Molokai mountains (see also comments on the distribution of *O. othello*).

Orsonwelles falstaffius, sp. nov. (Figs 4*F*, 5*A*–*C*, 9*A*–*E*, 33, 34, 55, 56)

Material examined

Holotype. Maui, Haleakala, Waikamoi Preserve, 21.viii.1995, coll. G. Hormiga & J. Coddington, c. 1860 m, 1 δ (USNM).

Paratypes. Maui, Haleakala, Waikamoi Preserve, 21.viii.1995, coll. G. Hormiga & J. Coddington, c. 1860 m, 6 3, 8 9 (USNM).

Additional material examined. **Maui:** (East): Haleakala, Waikamoi Preserve, 21.viii.1995, coll. G. Hormiga & J. Coddington, c. 1860 m, 3 δ , 10 \Im ; Haleakala, Hanawi NAR, Poo Uli cabin, 5.v.1995, coll. D. A. Polhemus, 1585 m, pyrethrin fog on mossy ohia roots, 4 \Im ; Haleakala, middle Kula pipeline road, 15.v.1998, coll. D. A. Polhemus, 1158 m, pyrethrin fog on mossy ohia roots, 1 \Im ; Lower Waikamoi, 8.xi.1996, coll. M. R., 1280 m, 1 \Im (BM); Upper Waikamoi, 21.xi.1996, coll. M. R., B. Thorsby & A. Bohonak, 1890 m, 2 δ , 1 \Im (BM); Carruthers Camp, Waikamoi, 17.xii.1992, coll. R. Gillespie, 1875 m, 1 δ (BM); Waikamoi, 28.x.1991, coll. R. Gillespie, 1329 m, 1



Fig. 33. Orsonwelles falstaffius, sp. nov. δ from Waikamoi Preserve (East Maui). *A*, Palp, ectoventral; *B*, same, ectal; *C*, same, dorsomesal; *D*, same, ventral, embolic division removed; *E*–*F*, embolic division; *G*, tibial trichobothria, dorsal (scale bars: 0.5 mm).

Diagnosis

𝔅; Waikamoi, 15.xi.1991, coll. R. Gillespie, 1329 m, 1 ♀; Waikamoi Flume, 24.ii.1991, coll. R. Gillespie, 1311 m, 1 𝔅, 1 ♀; below Eke, 21.ii.1991, coll. R. Gillespie, 1280 m, 1 ♀. MAUI (West): West Maui Mts, Puu Kukui, near Kaulalewelewe cabin, 23.viii.1995, coll. G. Hormiga & J. Coddington, *c.* 860 m, 5 𝔅, 12 ♀; West Maui Mts, Puu Kukui trail, 19.xii.1997, coll. H. L. Oppenheimer, 1615 m, 2 𝔅, 2 ♀; West Maui Mts, on Ridge above Honokahua Valley, 9.xii.1997, 1067 m, web on *M. polymorpha*, 1 ♀ (BM).

Males are diagnosed by the morphology of the terminal apophysis (Fig. 33*C*), which can be distinguished from the similarly shaped apophysis of *O. graphicus* by the margin of the concavity between the apical and basal processes, smooth in *O. graphicus* (Fig. 35*C*) but irregular in *O. falstaffius*

(Fig. 33*C*), and by the width of the apical process (widest in *O. falstaffius*). See also the Diagnosis of *O. macbeth*. For females see the Diagnosis of *O. macbeth*.

Description

Male (holotype)

Total length 9.86. Cephalothorax 4.96 long, 3.22 wide, 2.85 high. Sternum 2.79 long, 1.98 wide. Abdomen 4.90 long, 3.28 wide. AME diameter 0.28. Clypeus height 2.28 × one AME diameter. Chelicerae with 10–11 prolateral and eight retrolateral teeth. Femur I 7.56 long, $1.52 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 2–3 + 2. Metatarsus I trichobothrium 0.17. Pedipalp as in Figs 33*A*–*G*, 55*A*–*E*. Pedipalpal tibia with three prolateral and 3–4 retrolateral trichobothria.

Female (paratype)

Total length 11.28. Cephalothorax 5.27 long, 3.47 wide, 2.67 high. Sternum 2.85 long, 1.98 wide. Abdomen 7.07 long, 4.77 wide. AME diameter 0.28. Clypeus height $2.39 \times$ one AME diameter. Chelicerae with 11–12 prolateral and 9–10 retrolateral teeth. Femur I 7.07 long, $1.34 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 2–3 + 3. Metatarsus I trichobothrium 0.21. Epigynum as in Figs 34A–F, 56C–D.

Variation

Male cephalothorax ranges in length from 4.22 to 5.33 (n = 9). Female cephalothorax ranges in length from 5.27 to 6.20 (n = 10). Male total length ranges from 8.06 to 9.92 (n = 9). Female total length ranges from 10.42 to 11.84 (n = 10). The specimens from West Maui have a wider epigynal trunk, as seen in a ventral view, than those form East Maui.

Natural history

Orsonwelles falstaffius has been collected in rainforests between 860 and 1617 m elevation in West Maui and between 1281 and 1891 m in East Maui. Their web architecture is that typical of the genus (Fig. 9A-E). This species is very abundant in the rainforest of Waikamoi Preserve, where I have found a number of them feeding on moths. The largest webs had a main sheet 70–80 cm wide with guy lines up to 80 cm high. The live specimens of the West Maui populations were slightly lighter in colour than those from East Maui.

Etymology

The species epithet is derived from the Orson Welles film 'Chimes at Midnight' (1966), in which Welles played Falstaff.

Distribution

Endemic to the mountains of East and West Maui.

Orsonwelles graphicus (Simon, 1900), comb. nov. (Figs 4*C*, 10*A*–*E*, 35, 36, 57–59)

Labulla graphica Simon, 1900: 463, pl. 16, fig. 2 (male and female description).

Material examined

Syntype series. Kona, 1904.x.24.113–114, 2 ¢ (BMNH); Kona, 1904.x.24.115–116, 1 ¢, 1 juvenile (BMNH).

Additional material examined. Hawaii: Kohala Forest Reserve, 20°04'58.4"N 155°54'29"W, 26.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 1980 m, 1 9; Kahaualea Natural Area Reserve, 19°26'43.0"N 155°07'20.5"W, 24.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 680 m, 13 ♂, 37 ♀ (USNM, BM and 19°26′43.0″N ZMUC); Kahaualea Natural Area Reserve, 155°07'20.5"W, 29.viii.1995, coll. G. Hormiga, J. Coddington, c. 680 m, 9 9; Puu Makaala Natural Area Reserve, off Stainback Hwy, 19°33'54.6"N 155°13'53.7"W, 27.iv.1999, coll. G. Hormiga, N. Scharff, M. Arnedo, c. 680 m, 9 9; Laupahoehoe Natural Area Reserve, 4.vi.1998, coll. M. R.a, 1 &, 1 & (BM); Akaka Falls State Park, 5.i.1977, coll. V. Roth, c. 135 m, 1 ♀ (CAS); Kona, 1 ♂ (Fauna Hawaiiensis Collection, BM); (probably Hawaii), 1 9 (Simon's handwritten label reads '20054 Lab. graphica ES Im. Sandwich') (MNHN).

Diagnosis

Males are diagnosed by the morphology of the terminal apophysis (Fig. 35), which can be distinguished from the similarly shaped apophysis of *O. falstaffius* by the margin of the concavity between the apical and basal processes, smooth in *O. graphicus* but irregular in *O. falstaffius*; see also Diagnosis of *O. macbeth*. For females see the Diagnosis of *O. macbeth*.

Description

Male (from Kahaualea Natural Area Reserve)

Total length 6.67. Cephalothorax 3.28 long, 2.30 wide, 1.92 high. Sternum 1.71 long, 1.42 wide. Abdomen 3.38 long, 2.16 wide. AME diameter 0.26. Clypeus height 1.78 × one AME diameter. Chelicerae with nine prolateral and eight retrolateral teeth. Femur I 5.58 long, $1.70 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 2 + 2-3. Metatarsus I trichobothrium 0.19. Pedipalp as in Figs 35*A*–*F*, 57*A*–*F*. Pedipalpal tibia with 2–3 prolateral and three retrolateral trichobothria.

Female (from Kahaualea Natural Area Reserve)

Total length 8.80. Cephalothorax 4.40 long, 3.10 wide, 2.42 high. Sternum 2.23 long, 1.80 wide. Abdomen 4.46 long, 3.72 wide. AME diameter 0.22. Clypeus height $1.82 \times$ one AME diameter. Chelicerae with nine prolateral and 8–9 retrolateral teeth. Femur I 6.26 long, $1.42 \times$ length of cephalothorax. Femoral trichobothria (III + IV): 3 + 3. Metatarsus I trichobothrium 0.20. Epigynum as in Figs 36A-E, 58C-F.



Fig. 34. Orsonwelles falstaffius, sp. nov. A-D, G-H, \heartsuit , I-J, \diamondsuit , from Waikamoi Preserve (East Maui); E, \heartsuit from Waikamoi Flume (East Maui); F, \heartsuit from near Kaulalewelewe Cabin area (West Maui). A, E-F, Epigynum, ventral; B, same, caudal; C, same, cleared, ventral; D, same, dorsal; G, cephalothorax, frontal; H, J, cheliceral teeth; I, chelicera, frontal (scale bars: 0.5 mm, except G, I, 1.0 mm).

Variation

Natural history

Male cephalothorax ranges in length from 3.27 to 3.41 (n = 4). Female cephalothorax ranges in length from 3.72 to 4.40 (n = 6). Male total length ranges from 6.20 to 6.67 (n = 4). Female total length ranges from 8.06 to 9.86 (n = 6).

Orsonwelles graphicus has been collected in rainforests at elevations ranging from 135 to 1980 m. This represents the highest range in elevation of any *Orsonwelles* species. The lowest elevation record comes from a single female collected



Fig. 35. Orsonwelles graphicus (Simon) δ from Kahaualea Natural Area Reserve (Hawaii). *A*, Palp, ectoventral; *B*, same, ectal; *C*, same, dorsomesal; *D*–*E*, embolic division; *F*, tibial trichobothria, dorsal (scale bars: 0.5 mm).

at Akaka Falls (a fairly ecologically disturbed area at *c*. 135 m elevation). I could not find this species in the Akaka Falls area and their presence there may have been accidental, if so, the lowest elevation for this species is around 680 m. Their web architecture is that typical of the genus (Figs 10A-E). The adult webs often lack any understructure and the main sheet

seems to have a more pronounced concave-down shape. The largest webs had a dense mesh of guy lines more than 1 m high and main sheets were up to 57 cm wide. In contrast, the juvenile webs lack a funnel and have a mesh of silk lines under the main sheet. Kleptoparasitic *Argyrodes* sp. (at least two species) are common in the webs.



Fig. 36. Orsonwelles graphicus (Simon) A–F, \mathfrak{P} , and H, I, \mathfrak{F} from Kahaualea Natural Area Reserve (Hawaii); G, Fauna Hawaiiensis specimen from Hawaii. A, Epigynum, ventral; B, same, caudal; C, same, lateral; D, same, cleared, dorsal; E, same, ventral; F, I, cheliceral teeth; G, H, cephalothorax, frontal (scale bars: 0.5 mm, except A–C, G, 1.0 mm).

Distribution

Endemic to rainforests of the island of Hawaii.

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Fig. 37. Or sonwelles malus, sp. nov. from Waialae Cabin area (Kauai). A, δ Palp, ectal; B, same, ventral; C, same, paracymbium; D, apical end of embolic division; E, epigynum, ventral; F, same, ventrolateral.



Fig. 38. Or sonwelles malus, sp. nov. from Waialae Cabin area (Kauai). A, δ Spinnerets; B, same, PLS (note AG–FL triad in upper right corner); C, epiandrous fusules; D, same, detail; E; epigynum, caudal; F, same, detail of epigynal socket.



Fig. 39. Or sonwelles calx, sp. nov. δ from Laau Ridge (Kauai). A, Palp, ectal; B, same, mesal; C, apical end of embolic division; D, same, detail; E, spinnerets; B, same, PLS (arrow, aggregate and flagelliform spigot nubbins).



Fig. 40. Orsonwelles calx, sp. nov. δ from Laau Ridge and φ from Makaleha Mountains (Kauai). A, Epigastric fusules; B, same, detail; C, epigynum, ventral; D, same, lateral; E, same, ventral, detail of epigynal socket.

D



Fig. 41. Or sonwelles ventus, sp. nov. δ from Makaleha Mountains (Kauai). A, Palp, ectal; B, same, dorsomesal; C, same, paracymbium; D, E, apical end of embolic division; F, paracymbium.

E



Fig. 42. *A–B, Orsonwelles ventus*, sp. nov. \Im from Makaleha Mountains (Kauai); *C–F, O. arcanus*, sp. nov. \Im from Poamoho trail (Oahu). *A*, Epigynum, ventral; *B*, same, detail of epigynal socket; *C*, epigynum, ventral; *D*, same, caudal; *E*, same, lateral; *F*, spinnerets.



Fig. 43. Or sonwelles polites, sp. nov. δ from Mount Kaala (Oahu). A, Palp, ectoventral; B, same, dorsomesal; C, apical end of embolic division; D, suprategulum, distal end; E, paracymbium; F, spinnerets (arrow, aggregate and flagelliform spigot nubbins).



Fig. 44. Orsonwelles polites, sp. nov. A-E, δ from Mount Kaala (Oahu); F-G, δ from Palikea (Oahu). A, Palp, ventral, embolic division removed; B-E, embolic division; F, epiandrous fusules; G, same, detail.



Fig. 45. Or sonwelles polites, sp. nov. \Im from Mount Kaala (Oahu). *A*, Epigynum, ventral; *B*, same, caudal (arrow, epigynal plug); *C*, spinnerets; *D*, ALS; *E*, PMS; *F*, PLS.



Fig. 46. Orsonwelles polites, sp. nov. from Mount Kaala (Oahu); A–D, F–H, \Im ; E, \Diamond . A, Cephalothorax, frontal; B, same, lateral; C, same, ventral (arrow, sternum extended between fourth coxae); D, same, ventral; E, leg III tarsal claw; F, chelicera, ectal (note absence of stridulatory striae); G, femur III trichobothrium; H, femur III trichobothria (arrows).



Fig. 47. *Orsonwelles ambersonorum*, sp. nov. δ from Mount Tantalus (Oahu). *A*, Palp, caudoectoventral; *B*, same, ventral; *C*, same, dorsomesal; *D*, same, mesal; *E*, apical end of embolic division; *F*, paracymbium.



Fig. 48. Or sonwelles ambersonorum, sp. nov. A-D, δ , E, φ from Mount Tantalus (Oahu). A, Epiandrous fusules; B, same, detail; C, spinnerets; D, PLS (note AG–FL triad nubbins in loer right corner); femur III trichobothria (arrows).



Fig. 49. Orsonwelles ambersonorum, sp. nov. \Im from Mount Tantalus (Oahu). A, Cephalothorax, frontal; B, same, lateral; C, chelicera, ectal (note absence of stridulatory striae); D, epigynum, ventral; E, same, caudal; F, same, caudolateral (arrows, epigynal plug); G, PLS.



Fig. 50. Orsonwelles arcanus, sp. nov. δ from Poamoho trail (Oahu). A, Palp, ectoventral; B, same, mesoventral; C, same, dorsoectal; D, same, apical end of embolic division; E, embolic membrane; F, paracymbium.



Fig. 51. Orsonwelles othello sp. nov. δ from Kamakou Preserve (Molokai). A, Palp, ectoventral; B, same, ventral; C, same, dorsoectal; D, same, apical end of embolic division; E, same, detail; F, paracymbium.


Fig. 52. Orsonwelles othello, sp. nov. A-B, G, δ , C-F, \Im from Kamakou Preserve (Molokai). A, Epiandrous fusules; B, same, detail; C, epigynum, ventral; D, same, caudal; E, same, lateral; F, spinnerets; G, same (arrow, aggregate and flagelliform spigot nubbins).



Fig. 53. Orsonwelles macbeth, sp. nov. δ from Pepeopae trail (Molokai). A, Palp, ectoventral; B, same, ventral; C, same, dorsoectal; D, same, apical end of embolic division and suprategulum; E, paracymbium; F, spinnerets (arrow, aggregate and flagelliform spigot nubbins).



Fig. 54. Orsonwelles macbeth, sp. nov. A-B, δ , C-F, φ , from Pepeopae trail (Molokai). A, Epiandrous fusules; B, same, detail; C, epigynum, ventral; D, same, caudoventral; E, same, caudal; F, same, lateral.



Fig. 55. Orsonwelles falstaffius, sp. nov. δ from Waikamoi Preserve (East Maui). A, Palp, ectoventral; B, same, ventral; C, same, dorsoectal; D, same, apical end of embolic division and suprategulum; E, same, apical; F, spinnerets (note aggregate and flagelliform spigot nubbins).



Fig. 56. Orsonwelles falstaffius, sp. nov. A-B, δ , C-G, φ , from Waikamoi Preserve (East Maui). A, Epiandrous fusules; B, same, detail; C, epigynum, ventral; D, same, caudal; E, ALS; F, PMS; G, PLS.



Fig. 57. Orsonwelles graphicus (Simon) δ from Kahaualea Natural Area Reserve (Hawaii). A, Palp, ectoventral; B, same, ectal; C, same, dorsoectal; D, same, detail; E, same, apical end of embolic division and suprategulum; F, same, apical.



Fig. 58. Orsonwelles graphicus (Simon) A–B, δ from Kahaualea Natural Area Reserve (Hawaii); C–F, φ from Puu Makaala Natural Area Reserve (Hawaii). A, Epiandrous fusules; B, same, detail; C, epigynum, ventral; D, same, caudal; E, same, anteroventral; F, same, lateral.



Fig. 59. Orsonwelles graphicus (Simon) \Im from Puu Makaala Natural Area Reserve (Hawaii). A, Spinnerets; B, detail on piriform spigots and tartipores on ALS; C, ALS; D, PMS; E, PLS.

Appendix 1. Additional taxa examined

Afroneta sp.: Cameroon, north west Province, Menchum Division, near Lake Oku, *c*. 2150 m, 7–13.ii.1992 (Griswold, Larcher, Scharff & Wanzie, USNM, CAS, ZMUC).

Bolyphantes luteolus (Blackwall): Spain, Huesca, Jaca, San Juan de la Peña, 19.xii.1977 (C. Pedrocchi-Renault *et al.* USNM).

Ceratinops inflatus (Emerton): USA, California, Mendocino Co., Caspar, 7.iii.1954 (J. Helfer, AMNH).

Erigone psychrophila Thorell: USA, Alaska, Pt Barrow, 23.vi.1963 (R. F. Ashley, AMNH).

Haplinis diloris (Urquhart): New Zealand, Fiordland Cascade, 16.i.1975 (A.D. Blest, OM).

Laminacauda plagiata (Tullgren): Chile, Malleco, 3 km W Victoria, 100 m, mixed *Nothofagus* forest, 13.xii.1984–12.ii.1985 (S. & J. Peck, AMNH). *Linyphia triangularis* (Clerck): Germany, between Deutzand and Siegen, 9.viii.1964 (R. Crabill, USNM); France, Manche, Quettehou, 27.vii.1956 (USNM); Spain, Huesca., x.1986 (J. A. Coddington, USNM).

Microlinyphia dana (Chamberlin & Ivie): USA, Washington, Clallam Co., Elwha river near Altaire campground, Olympic N.P., 2.viii.1990 (G. Hormiga, USNM).

Novafroneta vulgaris Blest: New Zealand, S of Brighton, 17.vii.1974 (A. D. Blest, OM).

Sciastes truncatus (Emerton): Canada, NW Territories, MacKenzie, Stagg R. camp, 19 km SE Rae, 12.viii.1965 (J. & W. Ivie, AMNH).

Typhochrestus digitatus (O. P. -Cambridge): England, Whiteford Burrows, 29.ix.1965 (J. A. L. Cooke, AMNH).