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Coptotermes formosanus Shiraki, 1909 (Blattodea, Rhinotermitidae) established in Israel and world distribution of a major termite pest

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Abstract
The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, 1909, is a highly destructive structural pest endemic to East Asia. We report a land-based establishment of *C. formosanus* in Petah Tikva, Israel, over 6000 km from its nearest previous locality in China. The species' identity was confirmed by soldier morphology and by COI sequence data. In addition, a population discovered in 1992 in suburban San Diego, California, USA, remains viable. Marathon hosts the first infestation of *C. formosanus* in the Florida Keys. The world distribution of *C. formosanus* is presented, and the biogeography and mechanisms of spread of this termite are discussed.

Keywords
COI sequence, new localities, soldier morphology, world distribution

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Introduction

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, 1909, is endemic to eastern Asia. This highly destructive pest was first observed outside of Asia in Hawaii in 1909 (Swezy 1914) and was first collected in the continental United States in Charleston, South Carolina, in 1957 (Chambers et al. 1988). From there, the termite dispersed by anthropogenic transport throughout the southeastern USA from Texas to the west and North Carolina to the north (Fig. 1C; Appendix, Table A1). In 1992, a sizable population of *C. formosanus* was found in a neighborhood of La Mesa, California (Atkinson et al. 1993), which was reported to have persisted through 1997 following termiticidal treatments (Rust et al. 1998). Between 2010 and 2015, two separate samples of *C. formosanus* were collected around Freeport, Grand Bahama Island (Scheffrahn et al. 2015).

We herein report the establishment of *C. formosanus* in Petah Tikva, Israel, the first new and widely disjunct locality since those reported above. Other distant reports of *C. formosanus* in South Africa and Sri Lanka (Gay 1967) have now been discounted by Scheffrahn (2013) and Chouvenc et al. (2016a), respectively. Reports of *C. formosanus* from Kenya and Uganda (Wanyonyi et al. 1984) have also not been followed by more recent collections and should also be disregarded until proven otherwise.

Methods

All samples (Appendix, Table A1) are deposited in the University of Florida Termite Collection (UFTC), Davie, Florida. A soldier from the Israel colony was photographed as a multi-layer montage using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software (Fig. 2A, C). The maps (Fig. 1) were prepared using ArcMap v. 10.7.1.

DNA extraction. The head of a single worker served as the source of tissue for DNA extraction. The head was removed, dried for 5 min and placed into a solution of tissue lysis buffer (buffer ATL) and proteinase K (180 µl ATL and 20 µl proteinase K) from the DNeasy® Blood and Tissue Kit (Qiagen). The head was left to lyse for 24 h at 56 °C. Following lysis, eluate was transferred to a new 1.5 ml microcentrifuge tube and DNA extraction proceeded as per the manufacturer's instructions.

PCR parameters, sequence data, and analysis. To obtain COI sequence data, DNA template from specimens was amplified using the primers LCO1490 (5′ GGTCAACAAATCATAAAGATATTG 3′) and HCO2198 (5′ TCAGGGTGACCAAAAAATCA 3′) (Folmer et al. 1994). PCR reactions contained 5X GoTaq Flexi Buffer, 25 mM MgCl2, 10 mM dNTP's, 10 mM of each primer, 10% PVP 40, and 2.5U GoTaq Flexi DNA Polymerase, 2 µl DNA template, and sterile dH20 to a final volume of 25 µL. Thermal cycling conditions were as follows: 2 min initial denaturation at 95 °C, followed by 35 cycles of 30 sec denaturation at 95 °C, 30 sec annealing at 40 °C, 1 min 30 sec extension at 72 °C, followed by a 5 min extension at 72 °C. PCR products were run on a 1.5% agarose gel stained with GelRed and amplicons of the appropriate size were purified using the Exo SAP ITTM PCR Product Cleanup Reagent (ThermoFisher Scientific, Waltham, MA, USA). Purified PCR product was quantified using a NanoDropLite spectrophotometer (ThermoFisher Scientific, Waltham, MA, USA) and sequenced using the SeqStudio Genetic Analyzer (ThermoFisher). Contiguous files were assembled using DNA Baser (v. 4.36) (Heracle BioSoft SRL, Piteşti, Romania).

Results

Coptotermes formosanus Shiraki 1909

New records. ISRAEL • 1 colony subsample (includes soldiers and workers); Petah Tikva, Aminach Street; 32.0979, 034.8971; 42 m a.s.l.; 29 Jan. 2020; Tomer Lu: University of Florida Termite Collection (UFTC) no. MES21. UNITED STATES OF AMERICA • 1 colony subsample (includes soldiers and workers); La Mesa, Alpine Drive; 32.7644, −117.0106; 202 m a.s.l.; 10 Aug. 2018; Michael K. Rust; UFTC no. US1628. • 1 winged imago; California, La Mesa, Panorama Drive; 32.7629, −117.0068; 220 m a.s.l.; 10 Aug. 2018; Michael K. Rust; UFTC no. US1629. • 1 colony subsample (soldiers and workers); Florida, Marathon, Overseas Highway; 24.718, −081.072; 2 m a.s.l.; 24 Jul. 2017; Mark Weinberg; UFTC no. FL5104.

All the known localities of *C. formosanus* are given in Figure 1. All UFTC collection data and localities are available at Scheffrahn (2019) and Appendix, Table A1.

Identification. The soldier of *C. formosanus* can be identified by having two setae on each side of the fontanelle (Fig. 2B′) while the other two invasive species, *C. gestroi* (Wasmann, 1896) and *C. heimi* (Wasmann, 1902) have only a single setae on each side of the fontanelle (Roonwal and Chhotani 1989; Scheffrahn et al. 1990).

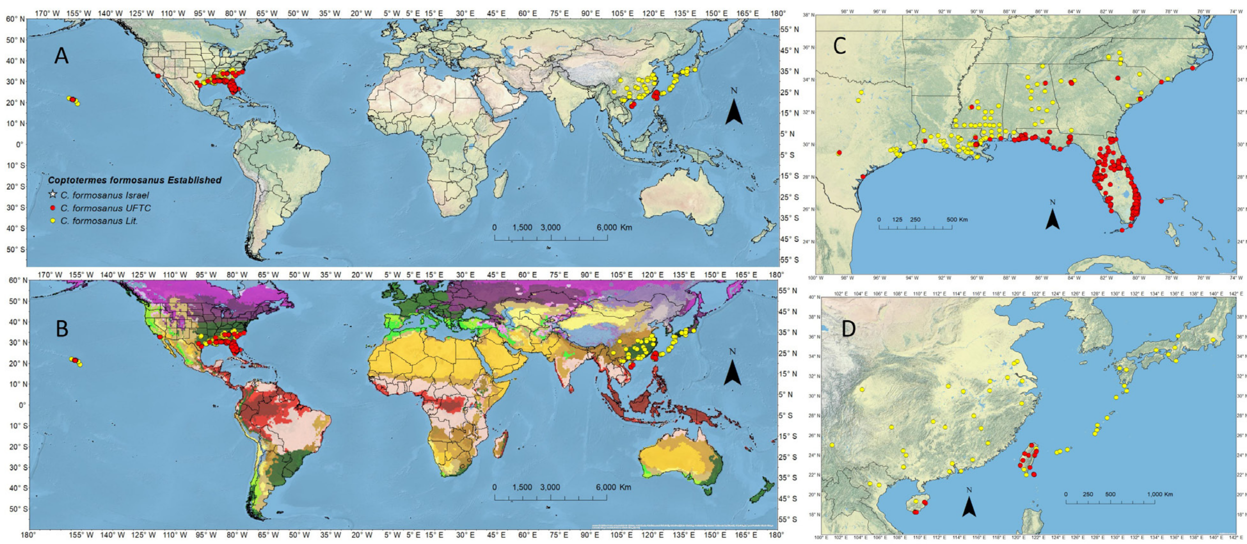

Figure 1. World distribution of *Coptotermes formosanus* based on published literature (Table 1) and the UFTC. **A.** Physical/topographic map. **B.** Köppen Geiger climate classification: (dark green = mild temperate, fully humid, and hot summer (includes central China, Japan, eastern Taiwan, and Hawaii); light green = mild temperate, dry and hot summer (includes western Israel and coastal southern California); brown = mild temperate, fully humid, and warm summer (includes western China and western Taiwan); pink = tropical, dry winter (includes Hainan China, Grand Bahama, and South Florida). See Kottek et al (2006). **C.** Detail of the southeastern United States. **D.** Detail of east Asia.

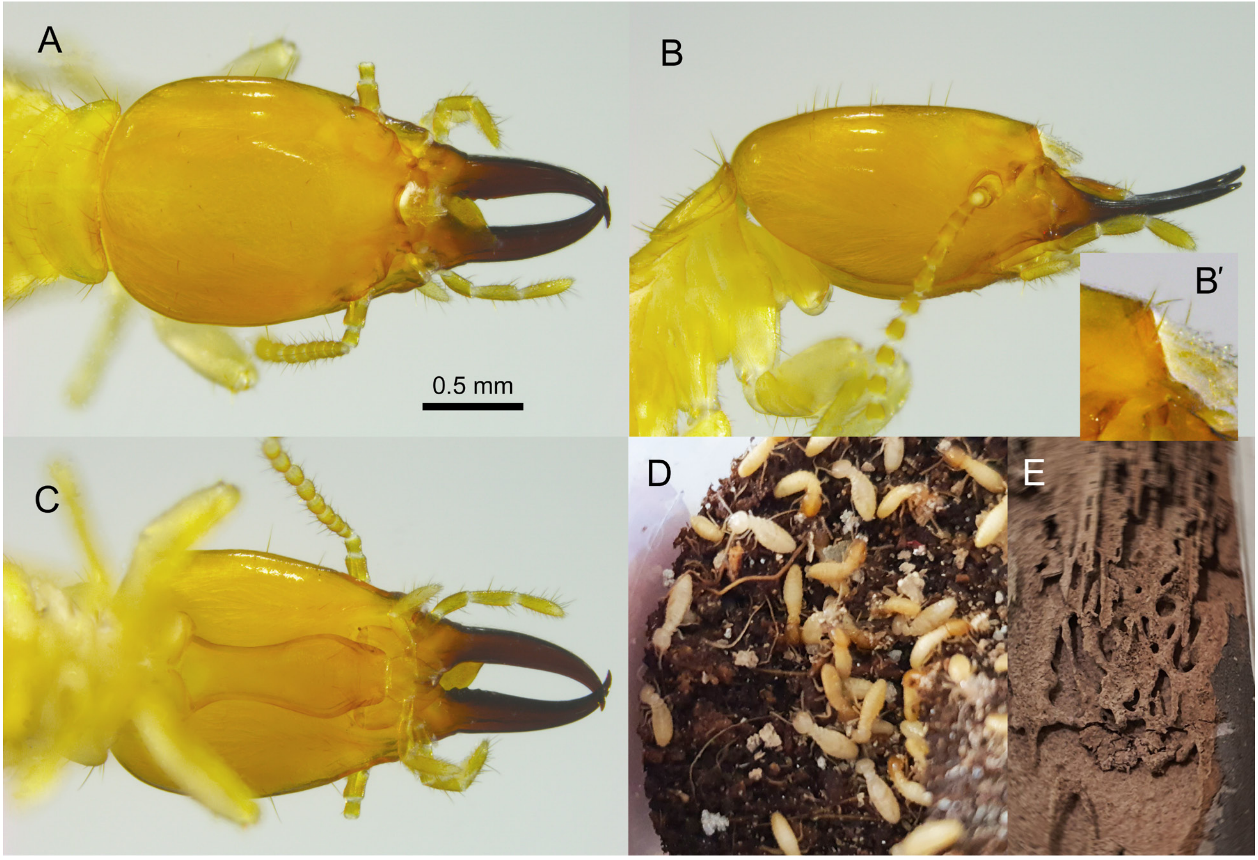

Figure 2. *Coptotermes formosanus* collected in Petah Tikva, Israel **A. C.** Soldier head capsule in dorsal, lateral, and ventral aspect. **B′.** Fontanelle showing four setae (2.5× scale relative to B). **D.** Foragers in collecting container. **E.** Partial carton (nest) material.

DNA Sequence Data. For the COI gene, a 655 bp sequence was generated (GenBank accession no. MT926002). The generated sequence in this study showed 98.93% shared identity with *Coptotermes formosanus* (GenBank accession no. KJ918309.1) at 99% query coverage and 98.93% shared identity with *Coptotermes suzhouensis* (a junior synonym of *C. formosanus*, Li et al. 2018; GenBank accession no. NC037018.1) at 99% query coverage.

Discussion

The current worldwide distribution of *C. formosanus*, based on literature localities (Appendix, Table A1) and UFTC records (Scheffrahn 2019; Appendix, Table A1) is limited to two main regions: eastern Asia and the southeastern USA. Also included are the Hawaiian Islands (probably all inhabited islands), isolated infestations in southern California, and now Israel (Fig. 1A). Eastern Asia and the southeastern USA experience a mild temperate and fully humid climate with hot summers (Köppen Geiger climate classification; Fig. 1B; Kottek et al. 2006). Hawaii, Hainan (China), Grand Bahama, and southern Florida (including the Florida Keys) transition into a tropical climate better suited for *C. gestroi* (Chouvenc et al. 2016a).

The climates for C. formosanus in southern California and the new discovery in Israel each experience Mediterranean conditions…….

The climates for C. formosanus in southern California and the new discovery in Israel each experience Mediterranean conditions contrary to climates of all other endemic or introduced localities. The marginal climatic suitability of *C. formosanus* in La Mesa is revealed by its very inhibited dispersal and colonization abilities there. A dye study of the La Mesa population suggests a single colony (Haagsma et al. 1995). The epicenter of the La Mesa infestation, inspected by RHS in 1992, was on the property of a US Navy employee whose belongings (including potted plants) were moved *en masse* from Hawaii over a decade earlier. During a comparable timespan, *C. formosanus* spread rapidly throughout Florida, reaching saturation in some areas (Chouvenc et al. 2016b). Therefore, it is plausible that the Israeli infestation may progress similarly to the La Mesa population.

The high degree of similarity between the sample collected in Israel and multiple accessions of *C. formosanus* confirm the identity of the termite as *C. formosanus*. Furthermore, the same level of similarity between the specimen and *C. suzhouensis* confirms this species status as synonymous to *C. formosanus*. For the five prime region of COI used in this study, variability of 0.2–2.0% is commonly seen at the intraspecific level and has been documented in a variety of insect taxa including aphids

(Xu et al. 2011), honeybees (Solorzano et al. 2009), flies (Prabhakar et al. 2012), and cockroaches (Ma et al. 2019). While the level of variability among species varies depending on the taxa being compared, generally 10% or greater sequence difference is indicative of species level difference. This has also been documented in cockroaches (Ma et al. 2019). However, some fly taxa have interspecific variability as low as about 5% (Boehme et al. 2012). Regardless, with the current specimen being less than 2% different from *C. formosanus*, it is evident the specimen collected from Israel is *C. formosanus*, representing a genetically distinct population in a new region.

Evidence is mounting that the eastern Asian localities of *C. formosanus* (Fig. 1D) all encompass the termite's endemic range based on phylogeographic similarities of the region (Qiu et al. 2011), Pliocene land bridges and genetic similarities of biota of the Ryukyu Taiwan island arc (Tokuda et al. 2012; Zhai et al. 2012), and the co-occurrence of conspecific beetle inquilines in *C. formosanus* colonies throughout this region (Iwata 2002; Maruyama et al. 2012).

Maritime transport is the most likely vehicle of transoceanic immigration beyond and within eastern Asia (Scheffrahn and Crowe 2011). Boat infestations are common in Florida, and alates, attracted to lights, fly from docked boats to land where they establish colonies (Hochmair and Scheffrahn 2010). We have no information on how *C. formosanus* was established in Israel (the site is 11 km inland), but the population was attacking wood throughout a four-story apartment building which had experienced dispersal flights in the recent past.

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Appendix

Table A1. Literature localities for *Coptotermes formosanus* shown in Figure 1.

Locality	Latitude, Longitude	Reference
CHINA		
Anhui	31.50, 117.09	Huang et al. 1989
Anqing	30.54, 117.07	Ruan et al. 2015
Fujian	25.24, 116.90	Huang et al. 1989
Guangdong	23.53, 115.36	Zhong and Liu 2003
Guangxi	22.83, 108.34	Chen et al. 2012
Guangxi	22.79, 108.37	Lin et al. 1994
Guangxi	23.99, 108.61	Zhong and Liu 2003
Guangzhou city	23.16, 113.28	Zhong and Liu 2003
Guizhou	26.84, 107.14	Huang et al. 1989
Hainan	19.35, 109.61	Huang et al. 1989
Hengyang	26.85, 112.55	Zhong and Liu 2003
Hong Kong	22.40, 114.16	Huang et al. 1989
Hsin hui	22.36, 112.99	Zhong and Liu 2003
Huangxi	24.46, 108.33	Zhong and Liu 2003
Hubei	30.99, 112.89	Huang et al. 1989
Hunan	27.40, 111.37	Husseneder et al. 2012
Jiangsu	33.28, 119.55	Huang et al. 1989
Jiangxi	28.00, 115.46	Zhong and Liu 2003
Jianhu	33.50, 119.84	Zhong and Liu 2003
Macau	22.20, 113.51	Huang et al. 1989
Nanjing	31.86, 118.88	Zhong and Liu 2003
Qionghai	19.25, 110.46	Li et al. 2009
Sanya	18.26, 109.51	Li et al. 2009
Sichuan	30.65, 104.16	Huang et al. 1989
Wuhan	30.45, 114.40	Zhong and Liu 2003
Wuwei	26.72, 116.20	Ruan et al. 2015
Wuxi	31.52, 120.36	Ruan et al. 2015
Yunan	25.03, 101.08	Zhong and Liu 2003
Zhejiang	29.24, 120.32	Huang et al. 1989
JAPAN		
Fukue	36.07, 136.12	Kanao et al. 2019
Honshu	36.16, 138.01	Huang et al. 1989
Iheya jima	27.04, 127.96	Kanao et al. 2019
Ishiki jima	24.40, 124.18	Kanao et al. 2019
Kagoshima	29.85, 129.87	Kanao et al. 2019
Kogoshima	31.03, 130.70	Kanao et al. 2019
Kumage	30.52, 130.92	Kanao et al. 2019
Kunimi	26.54, 127.92	Kanao et al. 2019
Kyushu	32.65, 130.89	Huang et al. 1989
Nansei	35.66, 139.69	Iwata 2002
Nasaki	32.80, 130.21	Kanao et al. 2019
Okayama	34.65, 133.92	Kanao et al. 2019
Okinawa	26.19, 127.70	Yamada et al. 2007
Oshima	27.79, 128.95	Kanao et al. 2019
Shikoku	33.74, 133.63	Huang et al. 1989
Tokyo (Machida)	35.54, 139.45	Tomioka et al. 2009
Uji	34.89, 135.80	Nakayama et al. 2004
Wakayama	34.21, 135.15	Yeap et al. 2014
Yaeyama	24.56, 124.92	Kanao et al. 2019
TAIWAN		
Chiayi	23.48, 120.44	Li et al. 2009
Hengchum	22.02, 120.76	Li et al. 2009
Hualien	23.97, 121.60	Li et al. 2009
Lanyu Is.	22.05, 121.55	Li et al. 2008
Nan'ao	24.68, 121.78	Li et al. 2009
Pingtung	22.55, 120.53	Li et al. 2009
Taichung	24.13, 120.67	Li et al. 2009
Tainan	23.00, 120.18	Li et al. 2009
Taitung	22.77, 121.13	Li et al. 2009
Taoyuan	25.01, 121.25	Li et al. 2009
UNITED STATES		
Alabama; Baldwin	30.76, 087.75	Stephan 2012
Alabama; Bullock	32.11, 085.70	Stephan 2012
Alabama; Calhoun	33.77, 085.82	Stephan 2012
Alabama; Chilton	32.87, 086.70	Stephan 2012
Alabama; Clay	33.30, 085.83	Stephan 2012
Alabama; Coffee	31.42, 085.99	Stephan 2012
Alabama; Covington	31.26, 086.43	Stephan 2012
Alabama; Cullman	34.14, 086.88	Stephan 2012
Alabama; Jackson	34.85, 085.98	Stephan 2012
Alabama; Jefferson	33.58, 086.88	Stephan 2012
Alabama; Lee	32.60, 085.35	Stephan 2012
Alabama; Lowndes	32.15, 086.64	Stephan 2012
Alabama; Mobile	30.82, 088.23	Stephan 2012
Alabama; Montgomery	32.23, 086.21	Stephan 2012
Alabama; Shelby	33.29, 086.66	Stephan 2012
Alabama; St. Clair	33.73, 086.31	Stephan 2012
California; La Mesa	32.76, 117.02	Woodson et al. 2001
Florida; Broward Co.	26.16, 080.18	Woodson et al. 2001
Florida; Citrus Co.	28.86, 082.55	Woodson et al. 2001
Florida; Dade Co.	25.72, 080.30	Woodson et al. 2001
Florida; Escambia Co.	30.56, 087.31	Woodson et al. 2001
Florida; Hillsborough Co.	27.90, 082.30	Woodson et al. 2001
Florida; Leon Co.	30.47, 084.23	Woodson et al. 2001
Florida; Martin Co.	27.09, 080.28	Woodson et al. 2001
Florida; Okaloosa Co.	30.57, 086.58	Woodson et al. 2001
Florida; Orange Co.	28.49, 081.32	Woodson et al. 2001
Florida; Palm Beach Co.	26.67, 080.14	Woodson et al. 2001
Florida; Santa Rosa Co.	30.72, 087.03	Woodson et al. 2001
Georgia; Cairo	30.88, 084.19	Woodson et al. 2001
Georgia; Chatham Co.	31.99, 081.11	Woodson et al. 2001
Georgia; Cobb Co.	33.95, 084.58	Woodson et al. 2001
Georgia; Dallas	33.92, 084.84	Woodson et al. 2001
Georgia; De Kalb Co.	33.78, 084.23	Woodson et al. 2001
Georgia; Fayette Co.	33.41, 084.50	Woodson et al. 2001
Georgia; Gwinnett Co.	33.94, 084.03	Woodson et al. 2001
Georgia; Harris Co.	32.72, 084.92	Woodson et al. 2001
Georgia; Lawrenceville	33.95, 083.99	Woodson et al. 2001
Georgia; Paulding Co.	33.91, 084.87	Woodson et al. 2001
Georgia; Tucker	33.85, 084.21	Woodson et al. 2001
Hawaii; Hawaii	19.37, 155.63	Woodson et al. 2001
Hawaii; Honolulu	21.32, 157.79	Woodson et al. 2001
Hawaii; Kauai	22.04, 159.54	Husseneder et al. 2012
Hawaii; Lanai	20.82, 156.90	Woodson et al. 2001
Hawaii; Maui	20.81, 156.39	Husseneder et al. 2012
Hawaii; Molokai	21.13, 156.97	Woodson et al. 2001
Louisiana; Amelia	29.65, 091.12	Messenger et al. 2002
Louisiana; Avery Island	29.88, 091.95	Messenger et al. 2002
Louisiana; Baton Rouge	30.45, 091.18	Messenger et al. 2002
Louisiana; Bayou D'Inde Pass	30.22, 093.31	Woodson et al. 2001
Louisiana; Beauregard	30.65, 093.35	Woodson et al. 2001
Louisiana; Cameron	29.90, 093.18	Woodson et al. 2001
Louisiana; Chalmette	29.95, 089.96	Messenger et al. 2002
Louisiana; Charon	30.03, 092.05	Messenger et al. 2002
Louisiana; Chauvin	29.50, 090.61	Woodson et al. 2001

Locality	Latitude, Longitude	Reference
Louisiana; Concordia	31.51, 091.63	Woodson et al. 2001
Louisiana; Coupee Blanks	30.55, 091.60	Woodson et al. 2001
Louisiana; Covington	30.48, 090.13	Messenger et al. 2002
Louisiana; Cut Off	29.50, 090.35	Messenger et al. 2002
Louisiana; Eden Isle	30.22, 089.79	Messenger et al. 2002
Louisiana; Eunice	30.57, 092.41	Woodson et al. 2001
Louisiana; Grand Isle	29.26, 089.96	Woodson et al. 2001
Louisiana; Harvey	29.91, 090.07	Messenger et al. 2002
Louisiana; Houma	29.58, 090.71	Messenger et al. 2002
Louisiana; Kenner	30.02, 090.26	Messenger et al. 2002
Louisiana; Kinder	30.48, 092.86	Woodson et al. 2001
Louisiana; Lafayette	30.22, 092.06	Messenger et al. 2002
Louisiana; Lake Charles	30.21, 093.24	Messenger et al. 2002
Louisiana; Laplace	30.06, 090.48	Woodson et al. 2001
Louisiana; Livingston	30.46, 090.74	Woodson et al. 2001
Louisiana; Metairie	29.97, 090.16	Messenger et al. 2002
Louisiana; Mossville	30.23, 093.30	Messenger et al. 2002
Louisiana; New Orleans	30.02, 090.10	Messenger et al. 2002
Louisiana; Noble	31.68, 093.68	Messenger et al. 2002
Louisiana; Norco	30.00, 090.40	Messenger et al. 2002
Louisiana; Ouachita	32.47, 092.15	Messenger et al. 2002
Louisiana; Pierre Part	29.91, 091.19	Messenger et al. 2002
Louisiana; Plaquemines	29.50, 089.69	Messenger et al. 2002
Louisiana; Prairieville	30.33, 091.00	Messenger et al. 2002
Louisiana; Raceland	29.71, 090.59	Messenger et al. 2002
Louisiana; Rayne	30.22, 092.27	Messenger et al. 2002
Louisiana; St. Gabriel	30.25, 091.10	Woodson et al. 2001
Louisiana; St. James	30.01, 090.46	Woodson et al. 2001
Louisiana; St. Martin	30.21, 091.67	Woodson et al. 2001
Louisiana; St. Rose	29.97, 090.32	Woodson et al. 2001
Louisiana; Sunset	30.40, 092.06	Messenger et al. 2002
Louisiana; Tangipahoa	30.59, 090.39	Woodson et al. 2001
Louisiana; Thibodaux	29.77, 090.85	Messenger et al. 2002
Louisiana; Vernon	31.10, 093.17	Woodson et al. 2001
Louisiana; W. Baton Rouge	30.47, 091.30	Woodson et al. 2001
Louisiana; Washington	30.84, 090.05	Woodson et al. 2001
Mississippi; Adams	31.50, 091.34	Sun et al. 2007
Mississippi; Amite	31.19, 090.81	Sun et al. 2007
Mississippi; Covington	31.64, 089.54	Sun et al. 2007
Mississippi; Forrest	31.19, 089.24	Sun et al. 2007
Mississippi; George	30.87, 088.64	Sun et al. 2007
Mississippi; Greene	31.22, 088.63	Sun et al. 2007
Mississippi; Hancock	30.42, 089.48	Sun et al. 2007
Mississippi; Harrison	30.53, 089.11	Sun et al. 2007
Mississippi; Hinds	32.28, 090.43	Sun et al. 2007
Mississippi; Jackson	30.55, 088.64	Sun et al. 2007
Mississippi; Jasper	32.01, 089.11	Sun et al. 2007
Mississippi; Jones	31.63, 089.18	Sun et al. 2007
Mississippi; Lamar	31.22, 089.51	Sun et al. 2007
Mississippi; Lauderdale	32.40, 088.68	Sun et al. 2007
Mississippi; Madison	32.64, 090.01	Sun et al. 2007
Mississippi; Marion	31.22, 089.84	Sun et al. 2007
Mississippi; Pearle River	30.77, 089.60	Sun et al. 2007
Mississippi; Perry	31.18, 088.99	Sun et al. 2007
Mississippi; Pike	31.19, 090.39	Sun et al. 2007
Mississippi; Rankin	32.26, 089.93	Sun et al. 2007
Mississippi; Smith	32.01, 089.50	Sun et al. 2007
Mississippi; Stennis Space Ctr.	30.36, 089.61	Sun et al. 2007
Mississippi; Stone	30.81, 089.12	Sun et al. 2007
Mississippi; Walthall	31.16, 090.13	Sun et al. 2007
Mississippi; Wilkinson	31.18, 091.30	Sun et al. 2007
North Carolina; Brunswick	34.06, 078.24	Woodson et al. 2001
North Carolina; Catawba	35.67, 081.22	Woodson et al. 2001
North Carolina; Rutherford	35.42, 081.90	Woodson et al. 2001
South Carolina; Beaufort	32.41, 080.74	Hathorne et al. 2000
South Carolina; Berkeley	33.18, 079.88	Hathorne et al. 2000
South Carolina; Charleston	32.80, 080.06	Hathorne et al. 2000
South Carolina; Darlington	34.34, 079.98	Hathorne et al. 2000
South Carolina; Dorchester	33.13, 080.42	Woodson et al. 2001
South Carolina; Orangeburg	34.34, 079.98	Hathorne et al. 2000
South Carolina; York	34.99, 081.18	Hathorne et al. 2000
Texas; Denton	33.22, 097.15	Smith et al. 2010
Texas; Fort Worth	32.73, 097.33	Austin et. al. 2006
Texas; Galveston Is.	29.29, 094.82	Howell et al. 1987
Texas; Pasadena	29.70, 095.21	Howell et al. 1987
Texas; Port Arthur	29.89, 093.92	Howell et al. 1987
Texas; Port Bolivar	29.38, 094.76	Howell et al. 1987
Texas; San Antonio	29.44, 098.55	Austin et. al. 2006
VIETNAM		
Vietnam; Hanoi	21.00, 105.88	Van Quang et al. 2012
Vietnam; Xuan Son Natl. Park	21.12, 104.97	Vu Quang et al. 2007