

Evolution and Extinction of Oceanic Land Crabs, an Example from the Hawaiian Islands

John Starmer and Gustav Paulay
 Division of Invertebrate Zoology
 Florida Museum of Natural History

Abstract

Although widespread among oceanic islands, in the remote Hawaiian Islands, land crabs are strikingly absent and this absence is the result of extinction, rather than dispersal limitation. Analysis of fossil remains show that an endemic *Geograpsus* was abundant before human colonization, grew larger than any congener, and extended further inland and to higher elevation than other land crabs in Oceania. Land crabs are major predators of nesting sea birds, invertebrates and plants, affect seed dispersal, and control litter decomposition; their removal can lead to large-scale shifts in ecological communities.



Figure 1. *Geograpsus crinipes* preys on a swiftlet on Palau. (left) Illustration of major claws of, in descending order, *Geograpsus crinipes*, *G. grayi* and *G. severnsi*, scale 10 mm. (right)

Methods

Fossil crab specimens from Hawaii were compared with specimens of the four known extant species of *Geograpsus*. Chelae, carapace, and 4th sternite (Fig 1, 2, 3) were measured in selected specimens. Twenty discrete morphological characters were also coded in each *Geograpsus* species and a species from the sister genus, *Grapsus tenuicrustatus*. Discrete character data were analyzed with PAUP v4.0, using maximum parsimony, with characters unweighted, character states unordered, with ACCTRAN character state optimization, treating multiple states as polymorphism, and running an exhaustive search. Bootstrap analysis with 10,000 replicates was used to evaluate clade robustness. Previous records of land crabs from the Hawaiian Islands were reviewed based on literature and selected specimen records.

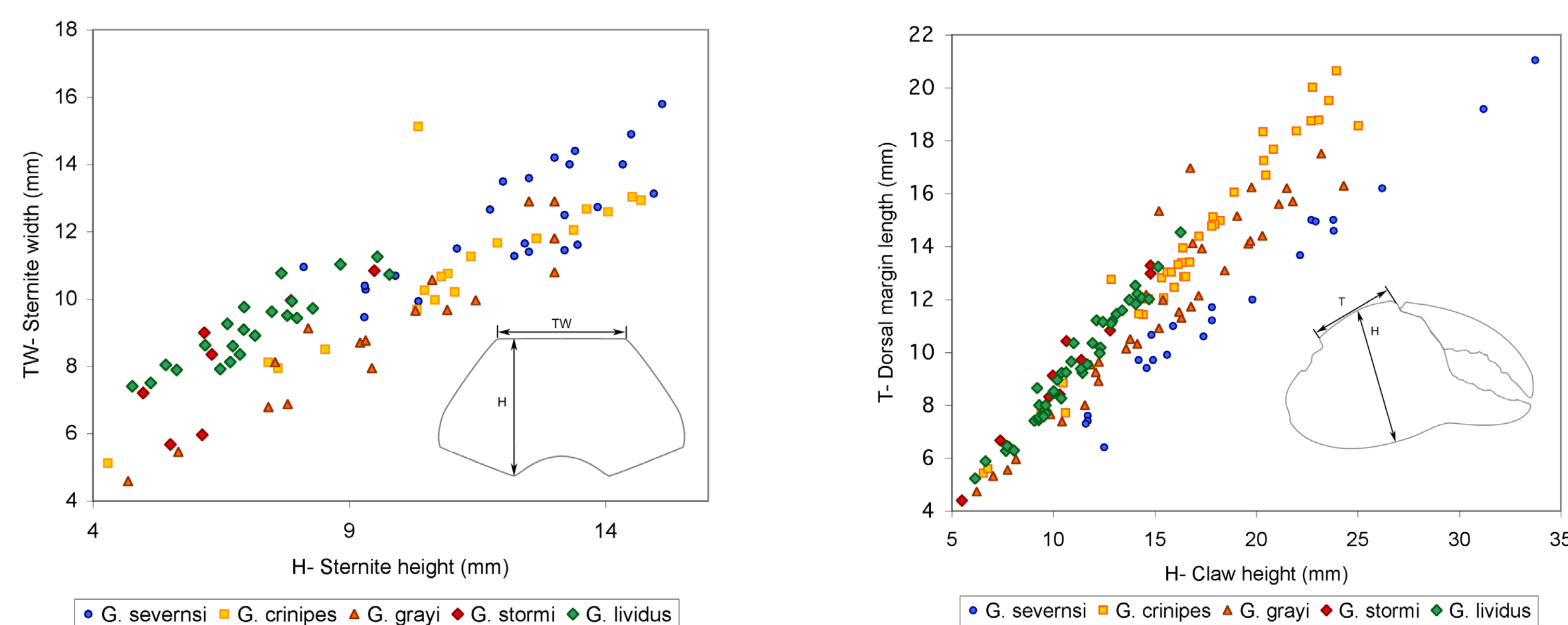


Figure 2. Examples of claw (left) and sternite (right) measurements used to investigate species differences in morphology.

Distribution

Geograpsus severnsi was widespread among, but endemic to, the Hawaiian Islands (Fig 3). Fossils are known from Hawai'i, Maui, O'ahu, and Kaua'i. Its sister species, *G. grayi*, ranges from the western Indian Ocean to the neighboring Line and Marshall Islands. *Geograpsus severnsi* extended further inland and to greater heights than any other land crab in Oceania. Fossils are known from nearshore settings to 950 m elevation. At 73 m elevation at Kiakeana Cave on Maui, remains of *G. severnsi* are common and co-occur with those of *G. crinipes*, indicating that like *G. grayi*, it overlapped in habitat with *G. crinipes* shoreward. The terrestriality of *G. severnsi* further supports its relation to *G. grayi*, the most terrestrial living grapsid (Fig.3).

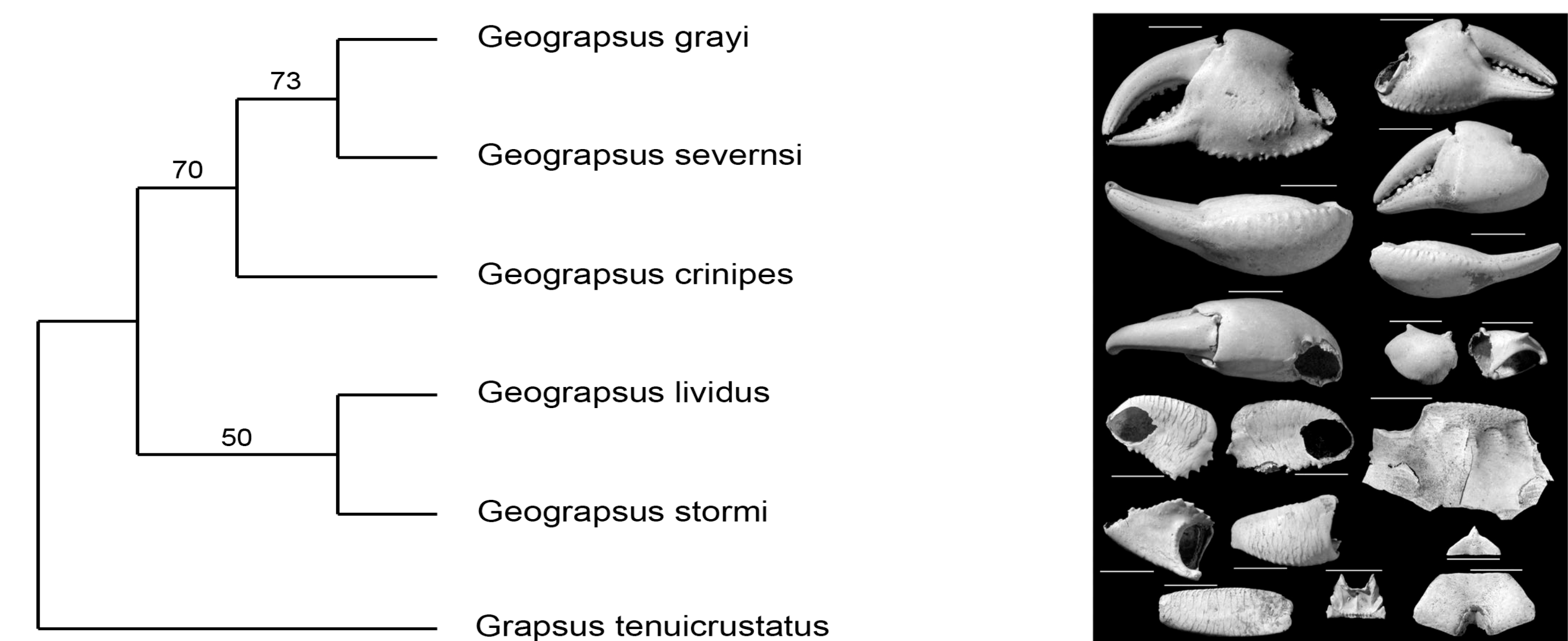


Figure 3. Single most parsimony tree with 10,000 bootstrap replicates for morphological data from all *Geograpsus* species (left). Holotype of *Geograpsus severnsi*, holotype male, scale 10 mm (right).

Extinction

Geograpsus severnsi is known only from the Hawaiian Islands, where the terrestrial biota are as well documented and no inland crabs have been recorded during historic times. Abundant *Geograpsus* fossils were taken from two excavations with well-dated stratigraphic context on Maui [1] and Kaua'i [2]. On Maui, *G. severnsi* survived to, but disappeared rapidly, after human arrival (C. Pittman (in litt. 11.IV.2004). On Kaua'i crabs are present in all pre-human layers, decrease in size during the early human period, and are absent from recent strata. *Geograpsus severnsi* appears to be the first documented crab extinction in the Holocene.

Acknowledgments

This study was made possible by fossil material collected by Mike Severns, David Burney, Cory Pittman, Storrs Olson, and Helen James. We thank Peter Davie, Lu Eldredge, Anne Fielding, Scott Godwin, John Hooper, Tohru Naruse, Peter Ng, Cory Pittman, and Chela Zabin for information on land crabs and Hawaiian records. Partially supported with funding from the US National Science Foundation (NSF DEB-0529724), Leila & William Brayfield Scholarship, and the Southwest Florida Fossil Club.

Literature

- Results published in Paulay G, Starmer J (2011) PLoS ONE 6(5): e19916.
 [1] James HF, Olson SL (1991) Ornithological Monographs 46:1–88.
 [2] Burney et al. (2001 Ecological Monographs 71: 615–641.