Search Theory and Convergent Spore Morphology

Jon E. Keeley

American Naturalist, Volume 124, Issue 2 (Aug., 1984), 307-308.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at http://www.jstor.org/about/terms.html, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Naturalist is published by University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/ucpress.html.

American Naturalist
©1984 University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

http://www.jstor.org/
Tue Apr 17 13:30:54 2001

SEARCH THEORY AND CONVERGENT SPORE MORPHOLOGY

Recently, Cox (1983) proposed that convergent evolution of aquatic spore morphologies is best explained as the result of selection for increased search efficiency and efficiency of anchorage. One of these convergent characteristics is large diameter spores and Cox argued that evolutionary trends toward large megaspores for water-dispersed pteridophytes are evident within the genus *Isoetes*. Cox claimed that submerged species of *Isoetes* have a significantly ($P < .05$) greater megaspore diameter than terrestrial species.

There are two major reasons why the analysis is flawed. Using Pfeiffer's (1922) monograph on *Isoetes,* Cox claimed that a "comparison of megaspore sizes for terrestrial versus aquatic species" is presented (Cox 1983, table 4). He presented, however, a selected group of 11 species from a monograph that includes 63 species (plus varieties). I have examined Pfeiffer's (1922) data and it is clear that by carefully selecting 11 other submerged and "terrestrial" species one could demonstrate exactly the opposite of what Cox demonstrated. If all species for which Pfeiffer presents habitat data are included in the megaspore diameter analysis there is no significant difference between habits (table 1*A*).

A second problem with Cox's analysis is his failure to consider life history characteristics of *Isoetes*. Based on his selection of species, apparently a "terrestrial" species was one which occurred out of water at some time in its life cycle. At least half of Cox's "terrestrial" species are in fact amphibious; they occur in seasonal pools, initially as submerged aquatics and, as the pools dry, as emergent aquatics and eventually as terrestrial plants. Since spore dispersal and sporeling production occurs early in the growing season (when the pools are filled), for Cox's purpose these species should be classified as submerged. Additionally, if consistent criteria had been used, one would not classify amphibious species such as *I. orcuttii* Eaton and *I. melanospora* Engelm. as terrestrial (Cox 1983, table 4) and *Stylites* Amstutz and *Pilularia* as submerged (Cox 1983, table 3). Most sources note (and personal observations support this) that the majority of *Stylites* colonies are not submerged. A comparison of *P. americana* A. Br. and *I. orcuttii* in southern California seasonal pools showed that both are submerged an average of 45 days per yr (Zedler and Ebert 1979). Regardless of how such species are categorized it is clear that there is no difference in megaspore diameter between perennially submerged and strictly terrestrial *Isoetes* (table 1*B*). Mean megaspore diameter would be even greater in the latter group if the recently described *I. hopei* Croft (Croft 1980) were included since it is a terrestrial species with one of the largest megaspores (875 μm) reported for the genus.

Thus, within the genus *Isoetes,* evolutionary trends in support of Cox's thesis are not evident. On the other hand, the patterns in *Isoetes* do not necessarily argue against his thesis. As pointed out by Cox, the group as a whole has very large megaspores. The vast majority of species are water-dispersed. The few

Am. Nat. 1984. Vol. 124, pp. 307–308.
© 1984 by The University of Chicago. 0003–0147/84/2402–0015$02.00. All rights reserved.

TABLE 1

COMPARISON OF MEGASPORE DIAMETER (maximum) FOR SPECIES OF *Isoetes* OF DIFFERENT HABITS

A. Species categorized according to the apparent criteria used in Cox (1983)

Habit	n	$\bar{X}$	SD	t	p
Submerged	15	596	107	.99	.20
"Terrestrial"	35	558	132		

B. Species categorized according to habit

Habit	n	$\bar{X}$	SD	F	p
Submerged perennially	15	596	107	.62	.54
Submerged seasonally or diurnally*	30	553	140		
Terrestrial	5	582	51		

SOURCE.—Data from Pfeiffer 1922; does not include varieties and formas and excludes 13 species for which insufficient data were presented.

NOTE.—Cox did not explain his criteria for categorizing species as submerged or terrestrial. Since Pfeiffer did not categorize species as submerged or terrestrial one must infer from the 11 species utilized by Cox what his criteria were. Apparently Cox classified as terrestrial any species that occurs out of water at some time during its life cycle. This criterion was used in table 1*A*.

* Tidal creeks.

terrestrial species may be secondarily derived with large megaspore size being conservatively maintained. The fact that the terrestrial species retain remnants of the four extensive lacunal chambers typical of the aquatic species, and the fact that at least one terrestrial species is capable of surviving submergence for extended periods (Keeley 1983), suggest an aquatic ancestry.

LITERATURE CITED

Cox, P. A. 1983. Search theory, random motion and the convergent evolution of pollen and spore morphology in aquatic plants. Am. Nat. 121:9–31.

Croft, J. R. 1980. A taxonomic revision of *Isoetes* L. (Isoetaceae) in Papuasia. Blumea 26:177–190.

Keeley, J. E. 1983. Lack of diurnal acid metabolism in terrestrial *Isoetes* (Isoetaceae). Photosynthetica 17:93–94.

Pfeiffer, N. E. 1922. Monograph of the Isoetaceae. Ann. Mo. Bot. Gard. 9:79–233.

Zedler, P. H., and T. A. Ebert. 1979. A survey of vernal pools of Kearney Mesa, San Diego County. Spring 1979. Progress report to California Department of Transportation in accord with CALTRANS Grant 06309 to San Diego State University Foundation.

JON E. KEELEY

DEPARTMENT OF BIOLOGY
OCCIDENTAL COLLEGE
LOS ANGELES, CALIFORNIA 90041

Submitted February 17, 1983; Accepted August 16, 1983