

Latitudinal variation in stipe hollowing in *Eisenia arborea* (Phaeophyceae, Laminariales)

PAUL G. MATSON* AND MATTHEW S. EDWARDS

Department of Biology, San Diego State University, San Diego, CA 92182, USA

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Morphological variation is common in kelps (Phaeophyceae, Laminariales) and often results from differences in environmental conditions. Stipe hollowing, in particular, occurs in several kelp species worldwide but to date has been investigated for only a few species and primarily at local scales. Here we describe the patterns of stipe hollowing both within and among populations of *Eisenia arborea* across 800 km of its distribution along the west coast of North America. Our results indicate that there are large latitudinal differences among populations in both the occurrence of stipe hollowing (i.e. frequency of hollow stipes within a population) and hollowing extent (i.e. length of the hollow cavity relative to stipe length) in *E. arborea* sporophytes. Stipe length varied among our study locations, with the most southern population exhibiting the tallest stipes, the most northern population exhibiting the shortest stipes, and the three central populations exhibiting intermediate stipe lengths. The occurrence of stipe hollowing and hollowing extent also varied along a latitudinal gradient, with the more southern populations exhibiting both increased frequencies of hollowing and greater hollowing extents. In fact, although hollowing occurred in almost all (97%) of the sporophytes examined at the most southern location, it was absent in the sporophytes examined at the most northern location. Finally, although stipe hollowing was more common in larger stipes across all locations because of the overwhelming effect of location on the occurrence of stipe hollowing, stipe length alone is not a suitable predictor when considered across this species range.

KEY WORDS: Baja California, distribution, *Eisenia arborea*, hollow stipe, kelp, Laminariales, latitudinal gradient, morphology

INTRODUCTION

Species that exhibit wide-ranging distributions often express variable morphologies when examined across large geographic areas (e.g. Cheshire & Hallam 1989; Azevedo *et al.* 1998; Trussell 2000; Hill & Hill 2002; Irie & Iwasa 2003). Marine algae, in particular kelps (Phaeophyceae, Laminariales), provide excellent examples of morphological variation resulting from differences in environmental conditions such as temperature, nutrient availability and hydrodynamic forces (e.g. Chapman 1973; Camus & Ojeda 1992; Miller *et al.* 2000; Serisawa *et al.* 2002; Duggins *et al.* 2003; Wernberg *et al.* 2003; Roberson & Coyer 2004). Although some kelp species exhibit small-scale variability in response to local environmental conditions, large-scale patterns coincident with latitudinal or longitudinal changes in oceanographic climate can be seen in others. For example, at Santa Catalina Island, CA, USA, Roberson & Coyer (2004) found *Eisenia arborea* (Areschoug) to express wide bullate blades and small holdfasts in areas of low hydrodynamic flow and narrow smooth blades and large holdfasts in areas of high flow, likely in response to nutrient uptake ability. Similar variation in blade morphology has been observed in *Laminaria longicuris* (De la Pylaie) in Nova Scotia, Canada (Gerard & Mann 1979), *Nereocystis leutkeana* (Mertens) Postels & Ruprecht in San Juan Strait, Washington, USA (Koehl & Alberte 1988) and *Macrocystis integrifolia* (Bory) in Barkley Sound, British Columbia, Canada (Hurd *et al.* 1997). Likewise, examination of 11 distinct morphological characters for *Ecklonia radiata* (C. Agardh) J.

Agardh at 11 locations along western and southern Australia and northwestern New Zealand found that each location exhibited a unique morphology with no consistent spatial patterns of variation among individual morphological characters (Wernberg *et al.* 2003). In contrast, along the California coast, USA, populations of *Egregia menziesii* (Areschoug) occurring north of Point Conception (34.58°N, 120.65°W) generally exhibit thick tough stipes and small blades, whereas populations occurring south of Point Conception are dominated by thin smooth stipes and large blades, likely because of latitudinal differences in hydrodynamic conditions and ocean climate (Blanchette *et al.* 2002). Whether such morphological variation leads to increased success of these species by increasing survival or productivity is not entirely clear, nor are the mechanisms responsible for causing this variation.

Kelp populations expressing both solid and hollow stipes have been described worldwide, and this morphological variation has been used to clarify taxonomic confusion within some genera – e.g. *Laminaria* in the north Atlantic (Mann 1971; Chapman 1973; Kain 1976). Along areas of the northeastern United States, *L. longicuris* produces hollow stipes in their second year of growth but not in their first year, which often confuses them with *Laminaria saccharina* (Lamouroux), a species that does not produce hollow stipes (Egan & Yarish 1988). Although the occurrence of hollowing is more prevalent in larger individuals, Kain (1976) suggests that stipe hollowing is also a result of living in areas of extreme shelter and low temperature (see also Chapman 1973, 1974). Similarly, Egan & Yarish (1988) suggest that algae with hollow gas-filled thalli are more adversely affected by mechanical stress and therefore should be more prevalent in sheltered ar-

* Corresponding author (pmatson@gmail.com).

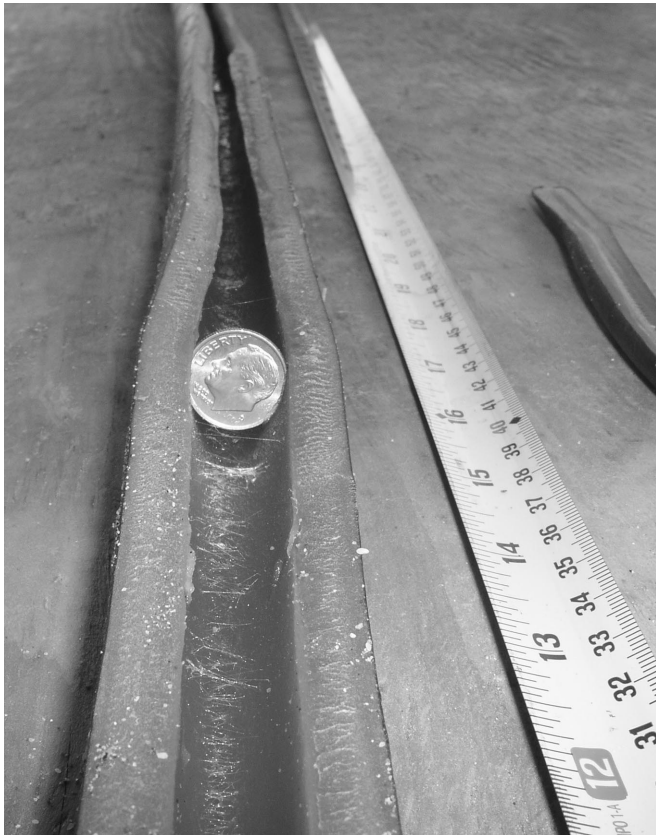


Fig. 1. Photograph of an *Eisenia arborea* stipe showing presence of a hollow cavity.

areas than exposed areas (see also Denny *et al.* 1998). In contrast, along the coast of Japan, *Ecklonia kurome* (Okamura) produces hollow stipes in areas of moderate wave exposure (Tsutsui *et al.* 1996), whereas along the west coast of North America, *Postelsia palmaeformis* (Ruprecht) exhibits hollow stipes and occurs in areas of moderate to high wave exposure (Abbott & Hollenberg 1976). Other northeast Pacific kelps, such as *N. leutkeana* and *Pelagophycus porra* (Leman) Setchell, exhibit solid stipes throughout most of their length, but hollow upper portions near their large pneumatocysts regardless of habitat (Abbott & Hollenberg 1976). Furthermore, although to our knowledge hollow stipes have not previously been described for *E. arborea*, observations along southern California, USA, and Baja California, Mexico, suggest that this species exhibits both hollow and solid stipes and that stipe hollowing might be more prevalent in southern populations. Here, we describe patterns of stipe hollowing in *E. arborea* at five locations spanning 800 km of its distribution along the west coast of North America. Furthermore, we quantitatively assess the relationship between stipe length and the occurrence of stipe hollowing and examine patterns of hollowing extent (i.e. length of the hollow cavity relative to stipe length) over this broad geographic range.

MATERIAL AND METHODS

Eisenia arborea (Alariaceae) occurs from Vancouver Island, British Columbia, Canada, to Isla Magdalena, BCS, Mexico

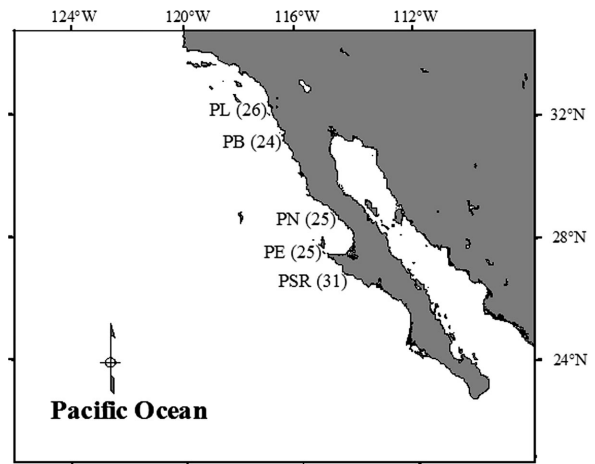


Fig. 2. Map of the west coast of California, USA, and Baja California, Mexico, showing the five study locations and number of *Eisenia arborea* collected in parentheses mentioned in the text are shown. PSR, Punta San Roque (27.17°N, 114.42°W); PE, Punta Eugenia (27.86°N, 115.06°W); PN, Punta Negra (28.77°N, 114.35°W); PB, Punta Banda (31.70°N, 116.67°W); PL, Point Loma (32.69°N, 117.26°W).

(Abbott & Hollenberg 1976) and is the dominant stipitate kelp, forming dense stands in the 5–15 m depth zone, along the west coast of Baja California, Mexico, south of Punta Banda (31.70°N, 116.67°W). *E. arborea* is a perennial kelp characterised by a 1–2 m stipe that bifurcates into two branches near its apex and supports numerous blades. Although *E. arborea* stipes are generally considered solid, observations made during previous sampling trips to this region (Edwards 2004) suggest that some individuals possess hollow stipes (Fig. 1), especially near the southern portion of the species' range (M.S. Edwards, personal observation). Thus, to examine broad-scale patterns in *E. arborea* stipe hollowing, five study locations separated by > 100 km and spanning approximately 800 km along the coasts of California, the United States and Baja California, Mexico (study locations correspond to those described in Edwards 2004), were sampled for *E. arborea* sporophyte morphology and the occurrence of stipe hollowing in July–September 2004 (Fig. 2).

Divers with SCUBA collected between 24 and 31 *E. arborea* sporophytes per location by cutting their stipes immediately above the holdfast and as close to the substrate as possible (see Fig. 2 for specific numbers collected per location). Individuals were selected by swimming a predetermined number of kick-cycles along randomly directed compass headings and collecting the first *E. arborea* sporophyte encountered with an apical bifurcation. This resulted in a wide range of sporophyte sizes being sampled within each location. Sporophytes were then removed from the substrate and transported to the shore where their stipe lengths were measured as the distance from the base to the apical bifurcation (hereafter all measurements are taken from the basal to apical direction). Each sporophyte was dissected by making a longitudinal incision along the stipe's main axis, thus splitting the stipe in two. The presence/absence of a hollow cavity (Fig. 1) was recorded, and if present, the cavity length was measured. Differences in stipe length among locations were examined

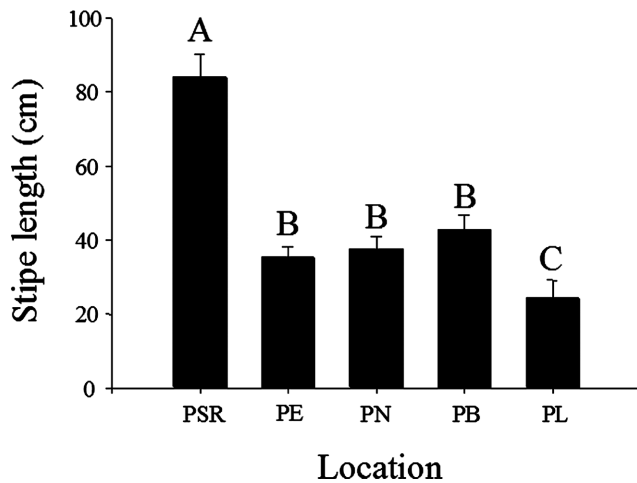


Fig. 3. Mean stipe length ($+ 1 s_x$) of *Eisenia arborea* sporophytes at each of the five study locations. Unique letters above the bars represent significant differences ($P < 0.05$) from other locations as determined by Fisher's LSD pairwise comparisons after ANOVA.

with a one-way ANOVA followed by Fisher's least significant difference (LSD) unplanned comparisons. Because stipe length varied among locations (see Results), the effect of stipe length on the occurrence of stipe hollowing was examined at each location separately with logistic regression. Hollowing extent, expressed as the proportion of the stipe that is hollow, was then determined by dividing the length of the cavity by the length of the stipe. Differences in hollowing extent among locations and the relationship between stipe length and hollowing extent were assessed across all locations with ANCOVA. Before testing, data were examined for homoscedasticity among locations by Cochran's test and for normality by graphical interpretation of the residuals. Data for stipe length were heteroscedastic and square root transformed, which corrected the problem.

RESULTS

Eisenia arborea stipe length varied significantly among the five sample locations (ANOVA: $F = 36.38$, $P < 0.001$, $\nu = 4$, 126), with the southernmost location (Punta San Roque) exhibiting the tallest stipes, the northernmost location (Point Loma) exhibiting the shortest stipes, and the central three locations (Punta Eugenia, Punta Negra and Punta Banda) exhibiting intermediate stipe lengths (Fig. 3). The frequency of sporophytes with hollow stipes also varied among locations, with the more southern populations expressing increased frequencies of hollowing (Fig. 4). Specifically, the majority of individuals at Punta San Roque (97%) and Punta Eugenia (80%) exhibited hollow stipes, whereas approximately half of the individuals (52%) at Punta Negra and one quarter (25%) of the individuals at Punta Banda exhibited hollow stipes. No sporophytes with hollow stipes were observed at the northernmost location, Point Loma. Stipe length did not significantly affect the occurrence of hollowing at either of the two southern locations (logistic regression: Punta San Roque, $P = 0.30$; Punta Eugenia, $P = 0.11$), likely because most of the individuals at these locations exhibited hollow stipes regard-

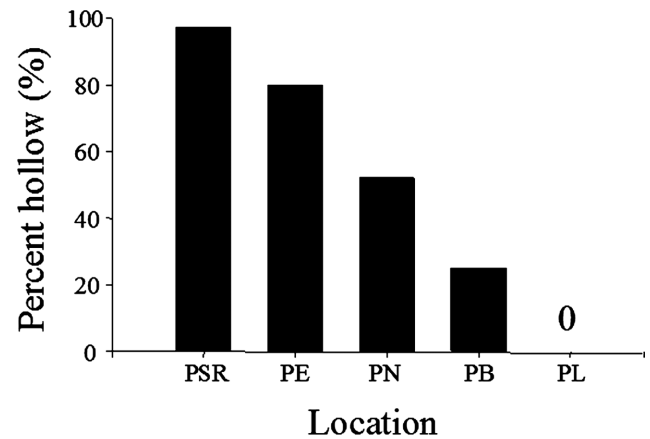


Fig. 4. Frequency of hollowing at each location expressed as the percentage of hollow stipes observed within the population.

less of stipe length. However, the single individual at Punta San Roque and four of the five individuals at Punta Eugenia that lacked hollow stipes were all shorter than the 95% confidence interval about the mean stipe length observed at those locations. The remaining individual at Punta Eugenia lacking a hollow stipe fell below the 80% confidence interval about the location's mean stipe length. In contrast, stipe hollowing at Punta Negra ($P = 0.04$) and Punta Banda ($P = 0.04$) was significantly more common in taller individuals.

Hollowing extent, expressed as the ratio between the length of the hollow cavity and the length of the stipe (i.e. percentage of stipe that was hollow), varied significantly among the four sample locations exhibiting hollow stipes (ANCOVA: $F = 7.18$, $P < 0.001$, $\nu = 3$, 44), with the more southern populations exhibiting greater hollowing extents (Fig. 5). Hollowing extent was also significantly greater in sporophytes with taller stipes across all locations (ANCOVA: $F = 7.33$, $P < 0.001$, $\nu = 1$, 44; Fig. 6), a pattern that did not vary among locations (Location \times Stipe length interaction: $F = 0.17$, $P =$

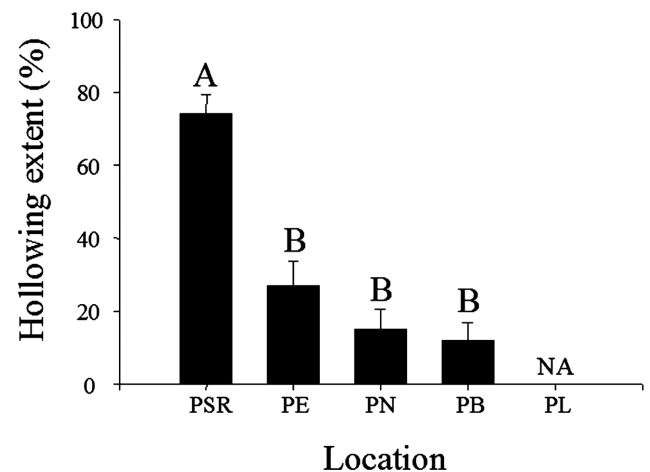


Fig. 5. Hollowing extent (expressed as the percentage of stipe that is hollow) of *Eisenia arborea* at each location. Unique letters above the bars represent significant differences ($P < 0.05$) from other locations as determined by Fisher's LSD pairwise comparisons following ANOVA.

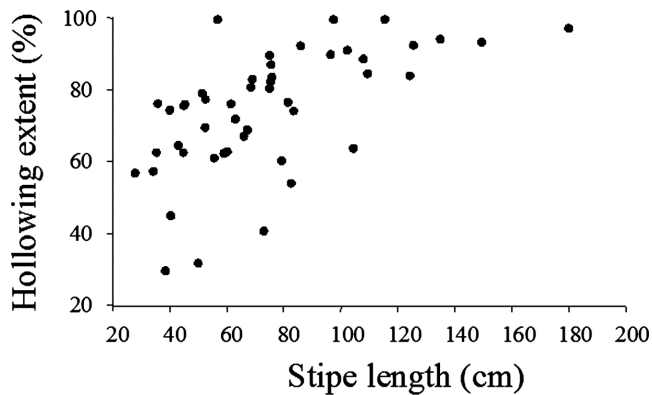


Fig. 6. Relationship between *Eisenia arborea* stipe length and hollowing extent (expressed as the percentage of the stipe that is hollow) across all locations that exhibited stipe hollowing.

0.912, $\nu = 3, 41$). Altogether, these results indicate large differences among locations in both the frequency and the extent of stipe hollowing in *E. arborea* sporophytes along the southern California, USA, and Baja California, Mexico, coasts. These differences include (1) more common stipe hollowing in southern populations regardless of stipe length, (2) absence of stipe hollowing in the southern populations only in the shortest individuals, (3) a relationship between stipe hollowing and stipe length in the northern populations, with stipe hollowing more common in taller individuals and (4) when present, greater hollowing extent in individuals with taller stipes regardless of location.

DISCUSSION

Previous studies have shown kelps to express morphological variation (Lubchenco & Cubit 1980; Camus & Ojeda 1992; Serisawa *et al.* 2002; Duggins *et al.* 2003; Wernberg *et al.* 2003) and genetic differentiation (e.g. Miller *et al.* 2000; Roberson & Coyer 2004) in response to differences in ocean climate. Stipe hollowing, in particular, has been observed in several genera within the Laminariales, likely in response to local hydrodynamic and temperature and nutrient conditions (Mann 1971; Chapman 1973; Kain 1976). In contrast, it has been suggested that for other species, hollowing might have occurred as part of speciation. For example, Bolton & Anderson (1987) suggest that *Ecklonia maxima* (Osbeck) Papenfuss, a southern Africa surface canopy-forming kelp with a hollow stipe, evolved from *E. radiata*, an understory canopy-forming kelp with a shorter, solid stipe within the last 3 million years. Still others suggest that stipe hollowing in some species results from biological interactions such as amphipod grazing (Chess 1993). However, we failed to observe any amphipods within the *E. arborea* stipes. Instead, we observed that medullary tissue found within solid *E. arborea* stipes was absent in hollow stipes (Fig. 1). In addition, we observed several, generally smaller, individuals exhibiting intermediate degrees of hollowing, in which the medulla was pitted with several small (< 1 cm) unconnected hollow spaces or in which hollowing was continuous but the medulla was only partially degraded. Although the mechanism remains unclear, it is our

belief that this loss of tissue is the direct cause of stipe hollowing.

We found the occurrence of stipe hollowing in *E. arborea* to vary geographically across a latitudinal gradient, with the more southern populations exhibiting greater frequencies of hollowing. In fact, the more northern populations not only contained progressively fewer individuals expressing hollow stipes, but hollowing was altogether absent in the northernmost location examined, Point Loma. However, in September 2004, we assessed the occurrence of stipe hollowing in 30 haphazardly selected *E. arborea* sporophytes at Santa Catalina Island, (33°27'N, 118°29'W), approximately 35 km off the coast of the southern California coast during an unrelated project. Although no measurements of stipe length or hollowing extent were made (we only assessed the presence or absence of hollowing), we found that 2 of 30 sporophytes examined (~7%) expressed hollow stipes. Although higher than that observed at Point Loma, this was still far lower than that observed in any of the southern locations. This is interesting when considering that Coyer *et al.* (2001) found *Macrocystis pyrifera* (Linnaeus) C. Agardh at Santa Catalina to be genetically similar to populations in southern Baja California. We recognize that our sampling design only encompasses a portion of *E. arborea*'s geographic distribution in the northeast Pacific, and we are therefore careful not to apply our results too rigorously beyond the study range.

Not only did the occurrence of hollow stipes vary geographically, but stipe hollowing was also generally more common in taller individuals. This relationship was more prevalent in the northern two locations that had hollow stipes (Punta Banda and Punta Negra). Although this relationship was not observed in the southern two locations (Punta San Roque and Punta Eugenia), likely because nearly all stipes were hollow regardless of stipe length, the only individuals at these locations expressing solid stipes were of the shortest sampled. Taller *E. arborea* were more likely to exhibit stipe hollowing, although the probability of a stipe becoming hollow varies from location to location along a latitudinal gradient regardless of stipe length. This pattern of the presence of a longer, hollow stipe is similar to that used to distinguish *L. longicuris* from *L. saccharina* (Mann 1971; Chapman 1973; Kain 1976; Egan & Yarish 1988) and *Ecklonia cava* (Kjellman) from *E. kurome* (Bolton & Anderson 1994). In addition, stipe length influenced hollowing extent as measured by the proportion of the stipe that was hollow (the length of the cavity relative to the length of the stipe). Taller individuals expressed greater proportions of their stipe as hollow, a pattern that was consistent among locations. We recognize that the evidence for this is only correlative; this study was not designed to identify the cause of stipe hollowing but instead to describe broad-scale patterns of stipe hollowing in *E. arborea* over a large portion of its geographic range. To our knowledge, this is the first report of stipe hollowing in this species. Although still unclear, the latitudinal patterns coincide with large-scale variation in light levels, water temperature, and nutrient availability. This could be important considering that previous studies have suggested that temperature might play a role in the formation of hollow stipes in some kelps (Bolton & Anderson 1987; Egan & Yarish 1988; Molloy & Bolton 1996). Generally speaking, ocean temperatures tend to be cooler in the northern portions of this range, although local atmospheric

and oceanographic conditions (e.g. coastal upwelling) might periodically override this pattern (Edwards & Estes, unpublished data). Consequently, we cannot conclude the cause or causes of stipe hollowing, and we recommend further investigation to resolve these issues.

It is not known whether the expression of hollow stipes has a fitness-related benefit (or cost). Duggins *et al.* (2003) found that morphological plasticity in two understory kelp species increased survival by reducing the effect of exposure from waves and currents. In addition to increasing survivorship, morphological variation has been shown to increase growth (Gerard & Mann 1979) and photosynthetic rates (Koehl & Alberte 1988). In the one study we know of relating stipe hollowing to sporophyte performance, Sjøtun & Gunnarsson (1995) found no difference in growth rates between solid and hollow-stipe morphologies of *L. saccharina* in Iceland. To date, no comparative studies of growth rates in *E. arborea* have been done across its range nor has any physiological assessment of the effects of stipe tissue loss on its growth and survival. However, hollow stipes might be important in supporting a taller canopy to access greater light intensities by providing increased buoyancy, as seen in the hollow midrib of *Alaria fistulosa* (Postels & Ruprecht) along the coast of Alaska and throughout the Aleutian archipelago, or flexibility to resist wave exposure, as in *E. maxima* along the coast of South Africa. Consequently, we believe that further studies regarding direct causes of hollow stipes and whether there are fitness-related effects should be encouraged.

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