

## **On the evolution of the mammalian baculum: vaginal friction, prolonged intromission or induced ovulation?**

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### **ABSTRACT**

The function of the mammalian baculum is a puzzling enigma in mammalian morphology. Three hypotheses for the evolution and persistence of the mammalian baculum have been proposed: the vaginal friction hypothesis; the prolonged intromission hypothesis; and the induced ovulation hypothesis. We tested these three hypotheses using phylogenetically corrected methods and data on North American carnivores. Baculum length was independent of sexual dimorphism and duration of copulation, thus refuting the vaginal friction and prolonged intromission hypotheses, respectively. Also, baculum length did not differ between induced ovulators and simultaneous ovulators, thus also refuting the induced ovulation hypothesis. We suggest that other aspects of carnivore life history, such as mating systems, may help explain the evolution of the mammalian baculum.

*Keywords:* baculum, comparative method, copulation duration, evolution, life history, North American carnivores, sexual dimorphism.

### **INTRODUCTION**

The baculum, or os penis, occurs in the orders Carnivora, Chiroptera, Primates and Rodentia (Hamilton, 1949). The development of the baculum is highly variable among species and its adaptive value, if any, remains controversial. Some authors have suggested that the os penis arose as a by-product of indirect selection and pleiotropy (Burt, 1960; Mayr, 1963). However, the energetic costs for the growth and maintenance of a baculum, as well as the risks of infection, fracture or breakage (Sanderson, 1950; Bolton, Camby & Boomker, 1996; Kierdorf, 1996), suggest that the baculum is adaptive. Furthermore, the high variability observed within families, and the observation that growth of the baculum reaches an asymptote late in reproductive life (Miller, Stewart & Stenson, 1998), indicates that, at least in some species, selection may operate on the development and maintenance of the baculum.

To date, three adaptive hypotheses have been advanced for the evolution of the baculum. The first hypothesis proposes that the baculum may provide additional rigidity to the erect penis to facilitate intromission (Long & Frank, 1968). This additional rigidity would be helpful for species in which mounting occurs before erection (e.g. Canidae) or species with strong sexual dimorphism (Long & Frank, 1968). For dimorphic species, the baculum would provide support to overcome the increased friction provided by the comparatively smaller size of the female's vaginal opening (first proposed by Long & Frank, 1968; the

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vaginal friction hypothesis). Although empirical tests are lacking, the vaginal friction hypothesis has received at least some acceptance (Patterson & Thaler, 1982; Krystufek & Hrabe, 1996).

A second hypothesis suggests that the baculum may assist in sperm transport (Ewer, 1973). More specifically, baculum size would increase in species that prolong intromission into the post-ejaculatory period (Dixon, 1987) and in species that have a single prolonged intromission instead of several short ones (Dixon, 1995). In both cases, the baculum would prevent occlusion of the urethral canal and consequent impairment of sperm flow (Ewer, 1973). This would be especially critical in species that adopt copulatory ties (e.g. Canidae). The prolonged intromission hypothesis was proposed to explain baculum size in primates (Dixon, 1987; Verrell, 1992) and possibly in some carnivores and pinnipeds (Dixon, 1995).

Finally, a third hypothesis suggests that the baculum may have evolved to provide additional penile rigidity to stimulate the reproductive tract of the female to induce ovulation, which would in turn increase the likelihood of successful fertilization (Greenwald, 1956). Although the induced ovulation hypothesis makes intuitive sense (Eberhard, 1985) several problems exist with it. For example, Felidae have small bacula and are induced ovulators (Foster, 1977; Schramm, Briggs & Reeves, 1994), whereas Canidae have large bacula and are spontaneous ovulators. Because induced ovulation may have evolved at the genus or family level, comparisons among species thus require the use of statistical analyses that control for phylogenetic effects (Felsenstein, 1985).

Phylogenetic effects may arise when species are not independent because of common ancestry. Considering non-independent data points increases the chances of committing a type 1 error (i.e. concluding an effect when none really exists). Phylogenetic effects are especially critical in evolutionary studies because morphological and life-history character changes or variation may have occurred either at the genus or family, instead of at the species, level (Harvey & Purvis, 1991). Existing comparative methods take one of two approaches: either they implement a correction for phylogenetic non-independence by manipulating the data prior to statistical testing (e.g. independent contrasts; Felsenstein, 1985) or the methods implement the correction at a later stage in the analysis, such as using computer simulation to estimate critical values that incorporate available information on phylogenetic structure (Garland *et al.*, 1993).

We used comparative analyses to test empirically the vaginal friction hypothesis, the prolonged intromission hypothesis and the induced ovulation hypothesis. We used data on North American carnivores because all members of this order possess a baculum and they exhibit a wide variation in baculum size (Burt, 1960). Furthermore, the morphometrics, reproduction and phylogeny of North American carnivores are well known (Ferguson, Virgl & Larivière, 1996; Bininda-Emonds, Gittleman & Purvis, 1999).

## METHODS

### Phylogeny and taxonomy

We used the phylogenetic tree proposed by Bininda-Emonds *et al.* (1999) and the taxonomy of Wozencraft (1993), with two exceptions. First, we considered skunks under the Mephitidae (Dragoo & Honeycutt, 1997). Secondly, we considered Eastern Spotted Skunk (*Spilogale putorius*) and Western Spotted Skunk (*Spilogale gracilis*) as separate species because of differences in reproductive mechanisms (e.g. presence or absence of delayed implantation; Mead, 1981) and because of phylogenetic differences (Dragoo *et al.*, 1993). The data set consisted of nine families, 31 genera and 52 species of carnivores, including pinnipeds (Table 1).

**Table 1.** Correlation statistics describing the relationship between corrected baculum length and sexual dimorphism and copulation duration for 50 species of North American carnivores. Regression coefficients were calculated assuming either no phylogenetic structure (ordinary least-squares correlation) or specified models of evolutionary change, gradual or speciational (Monte Carlo simulations)

	Conventional correlation			Gradual		Speciational	
	<i>n</i>	Observed <i>r</i>	<i>P</i>	Critical <i>r</i>	<i>P</i>	Critical <i>r</i>	<i>P</i>
Baculum length (corrected for body size) vs. sexual dimorphism							
All carnivores	42	0.163	0.33	0.581	>0.20	0.601	>0.20
Exclude felids	38	0.181	0.25	0.601	>0.20	0.609	>0.20
Baculum length (corrected for body size) vs. copulation duration							
All carnivores	19	0.397	0.08	0.581	>0.20	0.632	>0.20
Exclude felids	18	0.106	0.61	0.665	>0.20	0.643	>0.20

### Reproductive data and morphometrics

We obtained data from published sources on baculum length (mm), sex-specific body mass (kg), duration of copulation (minutes) and whether induced ovulation occurred. Reproductive and morphological data were obtained mainly from *Mammalian Species* articles (references in Appendix 1), complemented by data from Hayssen, van Tienhoven & van Tienhoven (1993) and Silva & Downing (1995). Information on induced ovulation was supplemented by reviews on carnivore reproduction (Wright, 1963; Colby, 1970, 1974; Weir & Rowlands, 1973; Milligan, 1982). For comparative purposes, we considered as induced ovulators any species for which induced ovulation has been reported, acknowledging that the distinction between the two groups may be a continuum (Weir & Rowlands, 1973) and that our analyses were limited by our current knowledge of the reproductive biology of North American carnivores. Dimorphism was calculated as male mass divided by female mass. Baculum information was completed with the works of Chaîne (1925), Didier (1946, 1947, 1949, 1950), Burt (1960), Long (1969) and Scheffer & Kenyon (1963). We used baculum length as an index of baculum size because age-related changes in baculum mass are greater than changes in length (Elder, 1951; Long & Frank, 1968). Length is also more readily available from the literature. Data were log-transformed (base 10) before analysis.

We used Monte Carlo simulations to estimate parameters for phylogenetic correlations and analyses of covariance. Monte Carlo algorithms incorporate phylogenetic structure by simulating character evolution (Garland *et al.*, 1993). Simulations were modelled using the postulated phylogenetic tree. Simulation values were restricted to limits defining biologically realistic bounds for each trait. Range limits for body mass were 2 g and  $1.7 \times 10^5$  kg, representing the approximate size limits for mammals (Nowak, 1999). Range limits corresponding to baculum lengths were 6–540 mm. Initial values were obtained from the average of all species values used in the analysis. We performed two sets of simulations: the gradual model assumed that expected variance of change was proportional to branch lengths; and the speciational model assumed change occurred only at speciation events and that all branch lengths were equal to one (Garland *et al.*, 1993). For each simulated data set ( $n = 1000$ ) we calculated phylogenetically corrected estimates of correlation and analysis of covariance parameters using general linear models.

### Hypotheses and predictions

We first tested whether baculum length increased with sexual dimorphism (vaginal friction hypothesis). Although morphological data linking female size with vaginal size were unavail-

able, we made the assumption that if 'vaginal friction' was a factor of importance in the development and persistence of a baculum, it should be of greater importance in species with greater dimorphism (as proposed by Long & Frank, 1968). To account for phylogeny, we used PDTREE (Garland *et al.*, 1993) to determine the slope from an analysis of independent contrasts with log-log data. We then divided baculum length by body mass raised to that scaling exponent (i.e. the slope from the independent contrast analysis). Finally, we correlated these mass-corrected baculum lengths with sexual dimorphism using PDSIMUL AND PDANOVA (Garland *et al.*, 1993).

Secondly, we tested whether greater duration of copulation was correlated with baculum length (prolonged intromission hypothesis). Again we used mass-corrected baculum lengths correlated with duration of copulation in PDSIMUL AND PDANOVA.

Finally, we tested the prediction that induced ovulators have longer bacula to stimulate the female's tract (induced ovulation hypothesis). We tested the null hypothesis of no difference in baculum length between the two groups (induced ovulators and non-induced ovulators) by phylogenetically corrected analysis of covariance (Garland *et al.*, 1993). For this analysis, baculum length was corrected for body mass by regressing baculum length against male body mass (ordinary least-squares regression).

Felids were found to be statistical outliers and as such could bias the final test statistic. We had hoped that simulations would provide null distributions that might account for their deviation, especially given the length of the branch that leads to felids (54 million years ago). However, the independent contrasts from PDTREE described felids as outliers in bivariate scatterplots. Therefore, we decided to present results both with and without felids. Further, we felt that because felids are a clade unto themselves, there are biological reasons to separate them from other Carnivora. Felids have small, perhaps vestigial, bacula (Didier, 1949) and the longest phylogenetic history of any North American carnivore family (Gittleman, 1986; Bininda-Emonds *et al.*, 1999).

For hypothesis testing, the statistics were calculated from the observed sample data in the conventional manner, and compared with the distribution of simulated test statistics (null distribution). The critical, or significance, value of each test statistic at the  $\alpha = 0.05$  level ( $F_c$ ) was obtained from the 95th percentile of the simulated distribution. The relevant  $F$ -statistics calculated for the observed data set (test for parallel slopes, differences between groups) were compared with the respective critical values (Garland *et al.*, 1993).

## RESULTS

### Vaginal friction hypothesis

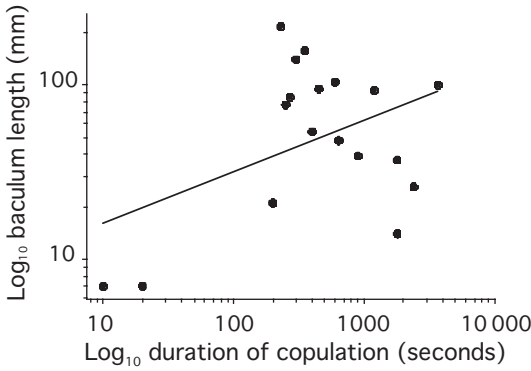
Phylogenetic independent contrasts were obtained from 42 species (six polytomies). The ordinary least-squares regression of log (baculum length, cm) on log (male mass, g) for 42 species of mammalian carnivores was given by:

$$\log(\text{baculum length}) = 0.773 + 0.190 \times \log(\text{male mass})$$

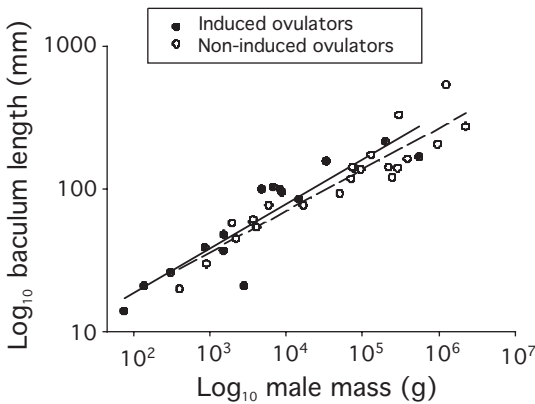
(d.f. = 40,  $r = 0.653$ ; Fig. 1). Parameter estimates obtained by both major axis (Harvey & Pagel, 1991) and reduced major axis (Ricker, 1973) regressions were almost identical and thus we present the results from least-squares regression. Baculum length was therefore corrected for mass by dividing by male mass to the exponent 0.1895 (slope).

We derived correlation coefficients for phylogenetic effects from the Monte Carlo simulation methods (Table 1). Regardless of the model of evolutionary change assumed, baculum length was independent of the sexual dimorphism index for all North American carnivores and for the same sample excluding felids as outliers ( $P > 0.05$  for all species; Fig. 2).





**Fig. 3.** Relationship between duration of copulation and baculum length for 18 species of North American carnivores [ $r^2 = 0.19$ ;  $\log(\text{baculum length}) = 1.21 + 0.293 \times \log(\text{duration of copulation})$ ].



**Fig. 4.** Relationship between male mass and baculum length for North American carnivores (except Felidae) that are induced ovulators ( $n = 13$ ) or not induced ovulators ( $n = 22$ ).

parallel slopes was not statistically significant (model  $F = 77.1$ , d.f. = 3,37;  $F_c = 0.29$ ,  $P = 0.59$ ), justifying the use of an ANCOVA. The overall difference between functional groups was not significant with non-phylogenetic methods, nor with phylogenetic methods with or without felids (Fig. 4 and Table 2).

## DISCUSSION

The existence of the mammalian baculum remains one of the most puzzling enigmas of mammalian morphology (Ruth, 1934; Ewer, 1973). Using phylogenetically corrected data on North American carnivores, we could not support the vaginal friction, prolonged intromission or induced ovulation hypotheses. Thus, none of the most cited hypotheses currently explain the presence and development of the baculum in mammalian carnivores.

Our results contradict the findings of Dixson (1995), who found a correlation between baculum length and duration of copulation in several species of carnivores and pinnipeds. However, several problems exist with his analysis. First, failure to use comparative methods could have produced spurious results due to phylogeny (Berrigan *et al.*, 1993). Studies of historical evolution require the use of statistical approaches that reconstruct ancestral character states using a phylogeny in combination with a statistical description of how the traits of organisms evolve (Pagel, 1999). The comparative method estimates the most probable characteristics of ancestral species, thereby allowing correlation and regression to investigate which features of organisms change with which other feature or with aspects of their environment. Hence, evidence is provided for the temporal order of changes in two traits, sug-

**Table 2.** Statistics for analysis of covariance (ANCOVA) testing the hypothesis of no difference between mass-corrected baculum length of induced ovulators and non-induced ovulators in the context of specified models of phenotypic change: no phylogeny (standard ANCOVA), gradual evolutionary change (proportional to branch lengths) or special evolutionary change (lengths of branches set equal to one). The covariate is body mass. The test of interest is the effect of reproductive ovulation (i.e. induced or non-induced). The critical *F*-statistic has 40 degrees of freedom

	Conventional ANCOVA				Monte Carlo simulations			
	Observed		Critical		Gradual		Special	
	d.f.	<i>F</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
All carnivores								
Covariate	1	2.10	4.02	0.16	90.7	>0.20	73.7	>0.20
Main effect	1	30.90	4.02	0.0001	20.4	0.02	18.5	0.01
Exclude felids								
Covariate	1	1.21	4.13	0.28	599.9	>0.20	368.8	>0.20
Main effect	1	212.10	4.13	0.0001	25.8	0.07	21.3	>0.20

gesting probable causal pathways. Secondly, the findings of Dixson (1995), that an enlarged baculum may serve to strengthen the penis and protect the urethra during prolonged intromissions, were supported solely by a comparison of felids (short intromission) with other carnivores (including pinnipeds; Dixson, 1995: 72, fig. 2). Comparing felids against other families may be inappropriate if felids are outliers (Dixson, 1995: 70, fig. 1). This also reinforces the importance of phylogenetic corrections to remove possible bias due to common descent (Harvey & Pagel, 1991). For example, in testing Dixson's (1995) hypothesis, if felids are statistical outliers due to evolved differences occurring at the family level, then results may not represent support for the prolonged intromission hypothesis. Although we did not re-analyse Dixson's (1995) data set, we suspect that statistical significance would no longer exist with proper phylogenetic corrections.

Our findings fail to provide a satisfying explanation for the development and persistence of the mammalian penis bone. Possibly, our ability to detect any relationships may have been weakened by our data set. However, data on duration of copulation are sparse in the literature, as are data for whether species are induced or spontaneous ovulators. We had initially considered a data set for world-wide carnivores, but rapidly realized that many data were missing and that many analyses would have consequently been reduced to North American carnivores because of the more detailed information on their life histories. Regardless, we were forced to conclude that the three hypotheses considered here fail to provide satisfactory explanations for the presence of a baculum in North American carnivores. Possibly, life-history traits such as mammalian mating systems may help explain the presence and variable development of the penis bone in mammalian carnivores. A link between mating systems and bacular development was recently proposed for pinnipeds (Miller, Jones & Stenson, 1999; Oosthuizen & Miller, 2000), although empirical tests for either pinnipeds or terrestrial carnivores remain unavailable. Further investigations are much needed to understand fully the adaptive value of the mammalian penis bone.

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**APPENDIX 1.** Body mass of males and females, sexual dimorphism (mass of males/mass of females) and baculum length (mm) for 52 species (nine families) of North American carnivores.

Family Species	Body mass (g)		Sexual dimorphism	Baculum length (mm)	Duration copulation (min)	Induced ovulation*
	Males	Females				
<b>Ursidae</b>						
<i>Ursus americanus</i> <sup>a</sup>	76 650	54 050	1.42	140	30	Yes
<i>Ursus arctos</i> <sup>b</sup>	200 000	118 670	1.69	216	23	Yes
<i>Ursus maritimus</i> <sup>c</sup>	550 000	225 000	2.44	168		Yes
<b>Odobenidae</b> <sup>d</sup>						
<i>Odobenus rosmarus</i>	1 246 000	690 000	1.81	540		No
<b>Phocidae</b> <sup>d</sup>						
<i>Cystophora cristata</i>	300 000	160 000	1.88	331		No
<i>Erignathus barbatus</i>	290 000	290 000	1.00	140		No
<i>Halichoerus grypus</i>	388 000	175 000	2.22	163		No
<i>Mirounga angustirostris</i>	2 250 000	900 000	2.88	274		No
<i>Phoca fasciata</i>	74 000	74 000	1.00	142		No
<i>Phoca groenlandica</i>	130 000	130 000	1.00	174		No
<i>Phoca hispida</i>	71 000	69 000	1.03	118		No
<i>Phoca largha</i>	97 000	86 000	1.13			No
<i>Phoca vitulina</i>	95 000	78 000	1.22	137		No
<b>Otaridae</b> <sup>d</sup>						
<i>Callorhinus ursinus</i>	220 000	43 000	5.81	142		No
<i>Eumetopias jubatus</i>	968 000	333 000	2.82	206		No
<i>Zalophus californicus</i>	245 000	82 000	2.99	121		No
<b>Procyonidae</b>						
<i>Bassariscus astutus</i> <sup>e</sup>	900	700		30		No
<i>Nasua narica</i> <sup>f</sup>	5900	3500	1.69	77		No
<i>Procyon lotor</i> <sup>g</sup>	6760	5940	1.14	104	60	Yes
<b>Mustelidae</b>						
<i>Enhydra lutris</i> <sup>h</sup>	33 350	23 600	1.41	157		Yes
<i>Gulo gulo</i> <sup>i</sup>	14 800	10 600	1.40	143	27	Yes
<i>Lontra canadensis</i> <sup>j</sup>	8760	7860	1.11	95	45	Yes
<i>Martes americana</i> <sup>k</sup>	860	565	1.52	39	90	Yes
<i>Martes pennanti</i> <sup>l</sup>	4760	2390	1.99	100	370	Yes
<i>Mustela erminea</i> <sup>m</sup>	138	57	2.42	21	20	Yes
<i>Mustela frenata</i> <sup>n</sup>	305	165	1.85	26	240	Yes
<i>Mustela nigripes</i> <sup>m</sup>	1500	1350	1.11	37	180	Yes
<i>Mustela nivalis</i> <sup>o</sup>	75	53	1.42	14	180	Yes
<i>Mustela vison</i> <sup>p</sup>	1523	852	1.79	48	64	Yes
<i>Taxidea taxus</i> <sup>q</sup>	8400	6400	1.31	99		Yes
<b>Mephitidae</b>						
<i>Conepatus mesoleucus</i> <sup>r</sup>	2168	1152	1.88	13		
<i>Mephitis macroura</i> <sup>s</sup>	806	717	1.12			
<i>Mephitis mephitis</i> <sup>t</sup>	2820	2 000	1.41	21	20	Yes
<i>Spilogale gracilis</i> <sup>r</sup>	483	397	1.22			No
<i>Spilogale putorius</i> <sup>u</sup>	399	283	1.41	20		No
<i>Spilogale pygmaea</i> <sup>v</sup>		230				
<b>Canidae</b>						
<i>Alopex lagopus</i> <sup>w</sup>	3620	3220	1.12	59		No
<i>Canis latrans</i> <sup>x</sup>	16 750	13 620	1.23	77	25	No
<i>Canis lupus</i> <sup>y</sup>	50 000	36 500	1.37	93	120	No
<i>Canis rufus</i> <sup>z</sup>	27 680	21 630	1.28			No
<i>Urocyon cinereoargenteus</i> <sup>aa</sup>	3700	3500	1.06	61		No
<i>Urocyon littoralis</i> <sup>ab</sup>	1950	1900	1.03	58		No

## APPENDIX 1. (Continued)

Family Species	Body mass (g)		Sexual dimorphism	Baculum length (mm)	Duration copulation (min)	Induced ovulation*
	Males	Females				
<i>Vulpes macrotis</i> <sup>ac</sup>	2200	1900	1.16	45		No
<i>Vulpes velox</i> <sup>ad</sup>	2440	2250	1.08			No
<i>Vulpes vulpes</i> <sup>ac</sup>	4100	3400	1.21	54	40	No
Felidae						
<i>Herpailurus yagouaroundi</i> <sup>af</sup>	5600	4500	1.24			Yes
<i>Leopardus pardalis</i> <sup>ae</sup>	11 200	7800	1.44	7	2	Yes
<i>Leopardus wiedii</i> <sup>ah</sup>	3600	3 000	1.20			Yes
<i>Lynx canadensis</i> <sup>ai</sup>	9870	8430	1.17	9		Yes
<i>Lynx rufus</i> <sup>aj</sup>	9600	6800	1.41	6		Yes
<i>Panthera onca</i> <sup>ak</sup>	94 900	67 000	1.42	8		Yes
<i>Puma concolor</i> <sup>al</sup>	60 000	40 000	1.50	7	1	Yes

a, Larivière (2001); b, Pasitschniak-Arts (1993); c, DeMaster & Stirling (1981); d, Bonner (1990), King (1983), Kovacs & Lavigne (1986; 1992); e, C. Hass (unpublished data); f, Gompfer (1995); g, Lotze & Anderson (1979); h, Estes (1980); i, Pasitschniak-Arts & Larivière (1995); j, Larivière & Walton (1998); k, Clark *et al.* (1987); l, Powell (1993); m, Fagerstone (1987); n, Sheffield & Thomas (1997); o, Sheffield & King (1994); p, Larivière (1999); q, Messick (1987); r, Patton (1974); s, Armstrong; Jones & Birney (1972); t, Verts (1967); u, Kinlaw (1995); v, Testa; Rybak & Baker (1981); w, Anthony (1997); x, Bekoff (1977); y, Mech; 1974); z, Paradiso & Nowak (1972); aa, Sullivan; 1956); ab, Moore & Collins (1995); ac, McGrew (1979); ad, Egoscue (1979); ae, Larivière & Pasitschniak-Arts (1996); af, Oliveira (1998a); ag, Richard-Hansen *et al.* (1999); ah, Oliveira (1998b); ai, Quinn & Parker (1987); aj, Larivière & Walton (1997); ak, Seymour (1989); al, Currier (1983).

\*Boone *et al.* (1998), Ewer (1973), Greensides & Mead (1973), Llewellyn & Enders (1954), Mead (1968), Mead *et al.* (1993), Wade-Smith & Richmond (1978), Wright (1963).