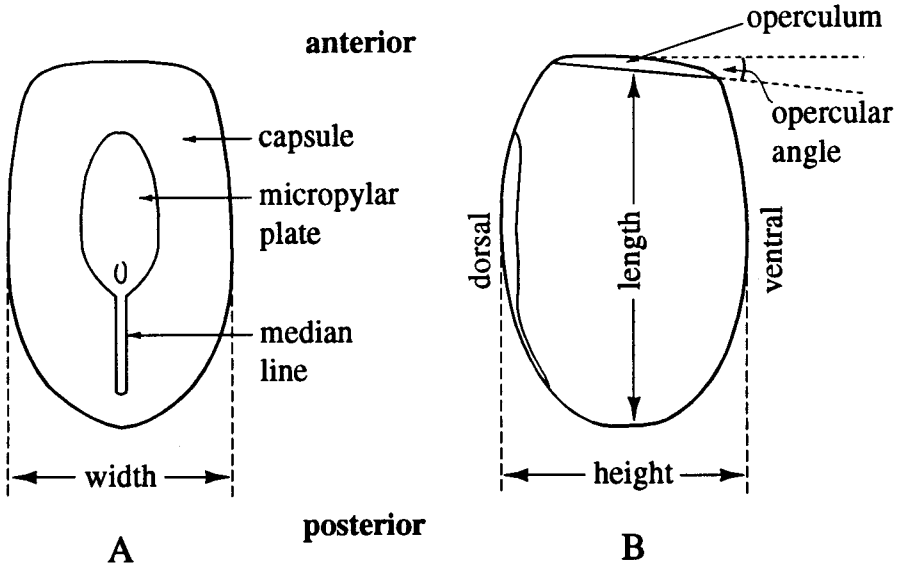
PHASMIDA (STICK INSECT) EGGS FROM THE EOCENE OF OREGON

by J. T. CLARK SELLICK

ABSTRACT. Three new taxa of fossil stick insects *Eophasma oregonense*, *E. minor* and *Eophasmina manchesteri*, are named from eggs found in the Eocene of Oregon. They are allocated to the tribe Anisomorphini and are the oldest known members of an extant family of the Phasmida.

THE Phasmida is an order of fossil and living insects which includes the stick insects and leaf insects. About 2000 extant species are known, and include some of the longest (over 300 mm) insect species known, if not the bulkiest. Their eggs are unique in possessing both a detachable anterior operculum and, on the dorsal surface, a distinct area of material constituting the micropylar plate. It has been indicated elsewhere (Sellick 1980) that this plate serves both as a location for the micropyles which carry the sperm, and as a respiratory area. It has also been shown that the combination of details of egg capsule and micropylar plate shape is characteristic of various subgroupings within the Phasmida. The eggs show a strong mimicry of plant seeds, which was thought originally to be only in shape. However, it has recently been shown also to extend in capitulate eggs to mimicry of elaiosomes, causing the eggs to be buried by ants in the same way as they treat seeds (Compton and Ware 1991; Hughes and Westoby 1992). The standard descriptive terminology for eggs of the Phasmida (Clark 1976) is illustrated with reference to an egg of the extant genus *Anisomorpha* (Text-fig. 1).



TEXT-FIG. 1. Terminology for the description of eggs of Phasmida (Anisomorphini). A, dorsal, and B, lateral views. The term 'egg' refers to the whole structure, and 'egg capsule' is the coating of the main part of the egg, excluding the operculum. The capitulum, not present on Anisomorphini eggs, is a raised structure on the operculum.

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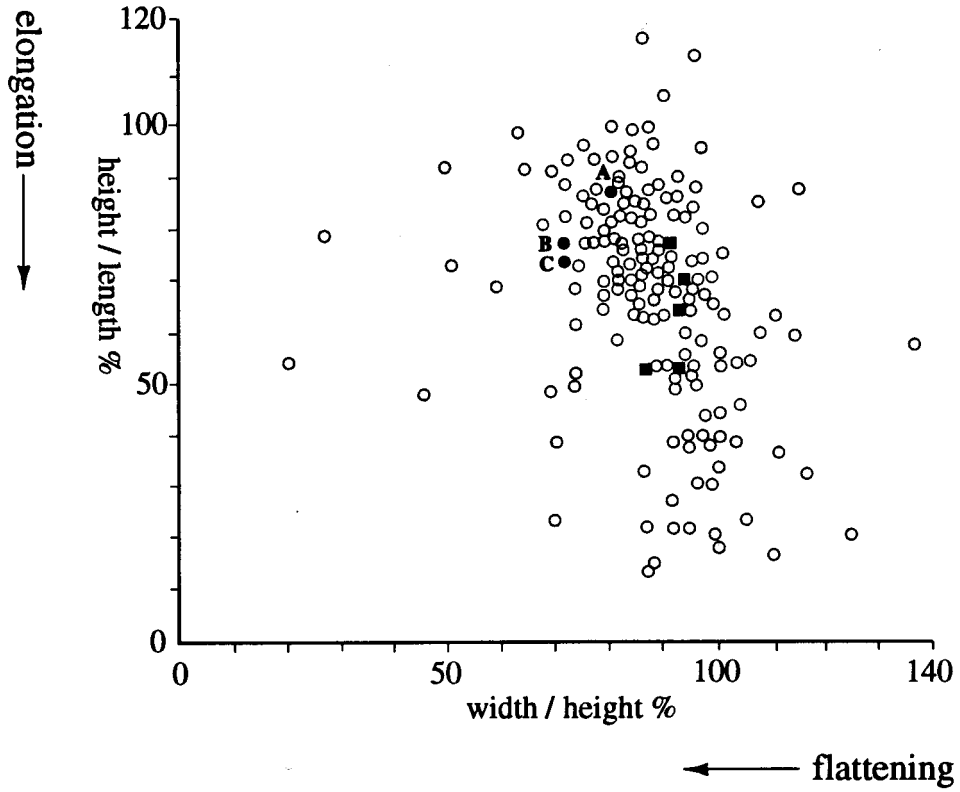
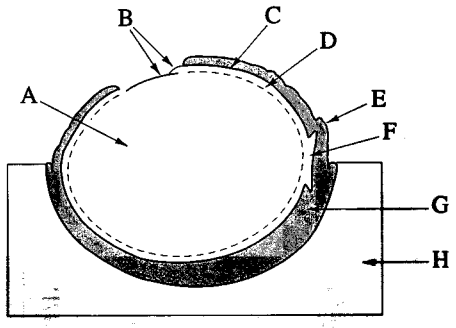


TEXT-FIG. 2. Shape distribution in known eggs of Phasmida. Black circles indicate fossil material: A, *E. oregonense*; B, *E. minor*; C, *E. manchesteri*. Black squares – extant Anisomorphini species; open circles – other known extant species.

The author was recently sent a series of small fossils from the Eocene Clarno Formation of Oregon, which were thought originally to be seeds. The fossils (around 3–4 mm in length) are completely replaced by silica, and preserve a reasonable amount of internal detail. In particular, they show that there is an internal micropylar plate. As in most modern phasmid eggs, the external plate is only slightly raised and can therefore only vaguely be delineated on the surface of the 'seed', and the internal plate was recognized only when the fossils were split parallel to their surface (Text-fig. 3). From this it is evident that the fossils are undoubtedly the remains of eggs of Phasmida and are the only known fossil eggs of this insect order.

Ten well-preserved specimens have been examined and it is concluded that they represent three species within two genera. All have a relatively generalized shape (Text-fig. 4), and are similar in capsule details, having a relatively small micropylar plate with a distinct median line extending posteriorly. Both genera show a feature unusual in extant phasmid eggs of having the operculum tilted ventrally, i.e. having a negative opercular angle. This is known only from a few extent genera, such as *Anisomorpha* and other members of the tribe Anisomorphini. However, the two fossil genera can quite clearly be distinguished from extant ones by details of the opercular structure.



TEXT-FIG. 3. Nature of the fossil material based on a section through *Eophasma oregonense* (UF 225–8686). A, pale silica infilling of egg capsule; B, inner layers seen due to surface fractures; C, outer surface of visible fossil, which is actually a fracture surface within capsule wall; D, inner capsule layer discernible in silica; E, indications of micropylar sculpturing; F, internal micropylar plate; G, full egg capsule wall replaced by dark mineral matter, probably carbonaceous remains of the original organic material permeated by silica; H, outer rock matrix.

MATERIALS AND METHODS

The fossils originated from the Nut Beds within the Clarno Formation, exposed in the John Day Fossil Beds National Monument, about 3 km east of Clarno, north-central Oregon, USA. The Clarno Formation is a non-marine accumulation of volcanic mudflows, tuffs and lavas. The Nut Beds locality is believed to represent a lake delta deposit. Based on radiometric dating, the age of the Nut Beds is *c.* 44 Ma and is thus middle Eocene (Manchester 1990). The eggs were associated with nuts, seeds and other plant debris. Dr Manchester informs me (*pers. comm.*) that they were obtained by prising out blocks of sediment which were then broken up. Remains were exposed in the matrix when intercepted by the resulting fracture planes. The percussion dislodged the silica casts and moulds from the matrix, sometimes leaving behind the outer wall layers. The internal structure was studied on fracture surfaces that developed during the extraction of the fossils. Further details of the palaeobotany and geology of the Nut Beds are given by Manchester (1981, 1990). The specimens are housed in the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA.

The dimensions are given in the descriptions, and in Table 1, to the nearest 0·05 mm. In the descriptions, the dimensions given of the egg are with the outermost layer of the capsule stripped off, which is probably not more than 0·10 mm in each case. A fragment embedded in matrix showed a fracture within 0·04–0·10 mm of the surface. In Table 1, therefore, the egg proportions are based on a uniform 0·10 mm being added to each surface. The volume of the eggs was calculated as follows:

$$\text{Volume} = \frac{(\text{length})}{2} \times \frac{(\text{width})}{2} \times \frac{(\text{height})}{2} \times 1{\cdot}33 \times \pi.$$

SYSTEMATIC PALAEONTOLOGY

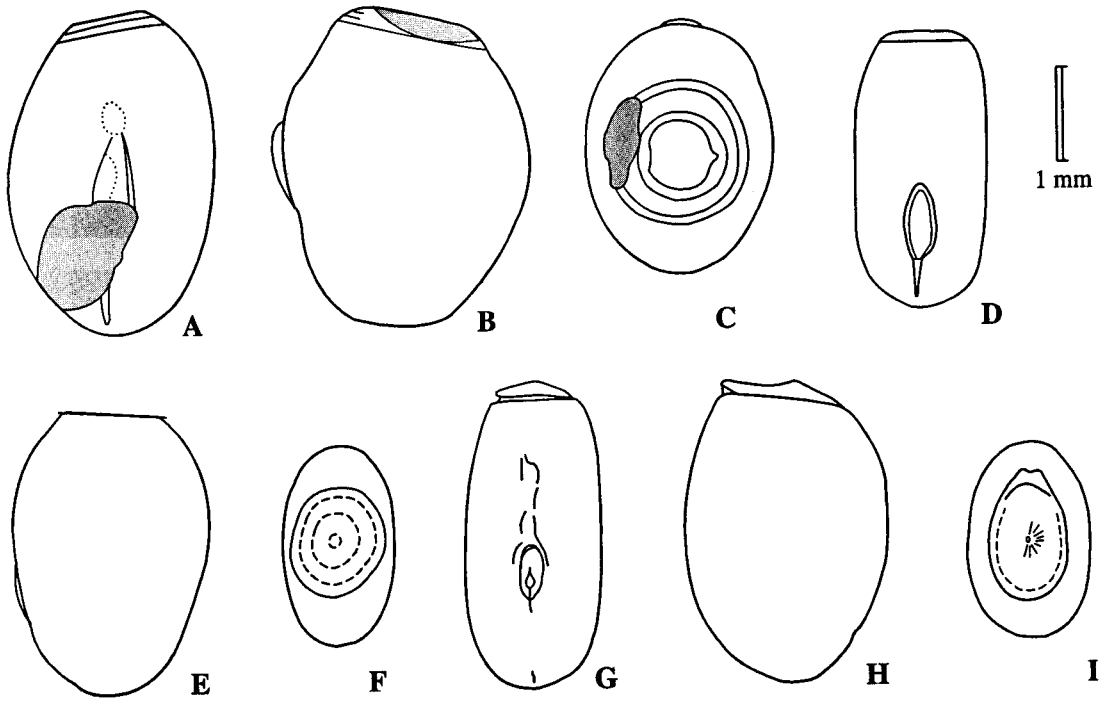
Class INSECTA
Order PHASMIDA Leach, 1814
Family PSEUDOPHASMATIDAE Kirby, 1896
Subfamily PSEUDOPHASMATINAE Kirby, 1896
Tribe ANISOMORPHINI Redtenbacher *in* Brunner von Wattenwyl and Redtenbacher, 1906
Genus EOPHASMA gen. nov.

Derivation of name. Combination of '*Eo*' from Eocene and '*phasma*' from the order name.

Type species. E. oregonense sp. nov.

TABLE 1. Dimensions (in mm) and operculum-type of Phasmida eggs; mpl = micropylar plate length, mpw = micropylar plate width, vol = egg volume (mm^3).

	Length	Width	Height	mpl	mpw	Operculum	w/h%	w/l%	h/l%	Vol
Eophasma oregonense										
UF 15768–6437 (holotype)	3·30	2·25	2·85	1·85	0·50	Ringed	80	72	89	11·1
UF 15768–6364 (paratype)	4·20	2·50	3·10	1·40	0·50	Missing	81	62	76	17·0
UF 15768–6366 (paratype)	3·75	2·40	3·10	1·20	0·60	Missing	78	67	85	14·6
UF 225–8686 (paratype)	3·35	2·45	3·10	—	—	Ringed	79	73	92	13·3
Eophasma minor										
UF 225–8689 (holotype)	3·15	1·55	2·20	1·00	0·35	Ringed	72	53	73	5·6
Eophasmina manchesteri										
UF 15768–6316 (holotype)	3·20	1·50	2·30	0·55	0·25	Conical	68	51	75	5·8
UF 15768–6314 (paratype)	3·10	1·45	2·05	0·50?	0·20	Conical	73	51	70	4·8
UF 15768–6317 (paratype)	2·80	1·50	2·20	0·40?	0·40?	Conical	70	58	82	4·8
UF 225–8688 (paratype)	2·70	1·50	2·00	0·30	0·20	Conical	77	60	78	4·2
UF 15768–6315 (paratype)	2·65	1·35	2·00	0·30	0·25	Conical	70	56	78	3·7



TEXT-FIG. 4. Holotypes of new species of eggs of Phasmida; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA. A–C, *Eophasma oregonense* gen. sp. nov.; UF 15768–6437. D–F, *Eophasma minor* gen. et sp. nov.; UF 225–8689. G–I, *Eophasmina manchesteri* gen. et sp. nov.; UF 15768–6316. A, D, G, dorsal views; B, E, H, lateral views; C, F, I, anterior (opercular) views.

Diagnosis. Eggs with roughly lozenge-shaped micropylar plate, in length about one third of capsule length, and with a well defined median line extending towards the posterior pole. Opercular angle negative. Operculum nearly flat with two or three slightly raised concentric rings.

Eophasma oregonense sp. nov.

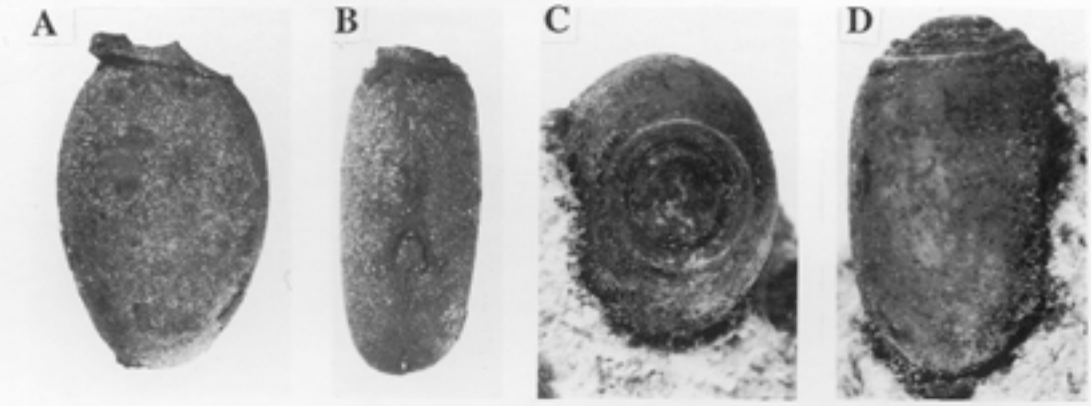
Text-figures 3, 4A–C, 5C–D, 6, 7A–B

Derivation of name. From Oregon, where the fossils were found.

Holotype. UF 15768–6437, from the middle Eocene Nut Beds of the Clarno Formation, John Day Fossil Beds National Monument, north-central Oregon, USA. Paratypes: UF15768–6364, 15768–6366, 225–8686 from the same horizon and locality.

Diagnosis. Eggs with capsule length 3·30–4·20 mm, width 2·25–2·50 mm, height 2·85–3·10 mm. Capsule volume 11·1–17·0 mm^3. Proportions: width/height 79–81 per cent; width/length 62–73 per cent; height/length 76–92 per cent.

Remarks. This is the commoner *Eophasma* species found in the Nut Beds, being represented by four specimens.



TEXT-FIG. 5. Eggs of Phasmida; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA; ×12·5. A–B, *Eophasmina manchesteri* gen. et sp. nov.; UF 15768–6316; lateral (A) and dorsal views (B) of holotype. C–D, *Eophasma oregonense* gen. et sp. nov.; UF 225–8686A; anterior (opercular) view (C) and lateral view (D) of specimen before sectioning.

Eophasma minor sp. nov.

Text-figures 4D–F, 7C

Derivation of name. From the small size of the eggs.

Holotype. UF 225–8689, from the middle Eocene Nut Beds of the Clarno Formation, John Day Fossil Beds National Monument, north-central Oregon, USA.

Diagnosis. Egg with capsule length 3·15 mm, width 1·55 mm, height 2·20 mm. Capsule volume 5·6 mm^3. Proportions: width/height 72 per cent; width/length 53 per cent; height/length 73 per cent.

Remarks. Only one specimen of this species was found. It is distinguished from *E. oregonense* by being distinctly smaller, narrower and more elongated.

?Tribe ANISOMORPHINI Redtenbacher *in* Brunner von Wattenwyl and Redtenbacher, 1906

Genus EOPHASMINA gen. nov.

Derivation of name. Diminutive of *Eophasma*.

Type species. *E. manchesteri* sp. nov.

Diagnosis. Eggs with small rounded micropylar plate, one sixth or less of the capsule length, and with a less distinct median line than in *Eophasma*. Opercular angle negative. Operculum raised in a shallow cone with a peripheral ring.

Remarks. This genus is distinguished from *Eophasma* mainly by the size and shape of the micropylar plate, the less distinct median line, and the raised operculum. *E. manchesteri* is the commonest species of the phasmid eggs found in the Nut Beds, with five specimens having been found.

TEXT-FIG. 6. *Eophasma oregonense* gen. et sp. nov.; UF 225–8686; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA; transverse section through egg, dorsal surface with micropylar plate (arrowed) at top; ×12·5.

TEXT-FIG 7. Eggs of Phasmida, viewed under SEM; Nut Beds, Clarno Formation (middle Eocene); John Day Fossil Beds National Park, Oregon, USA. A–B, *Eophasma oregonense* gen. et sp. nov.; UF 15768–6364; dorsal (A) and dorso-posterior views (B); ×10. C, *Eophasma minor* gen. et sp. nov.; holotype, UF 225–8689; dorso-lateral view; ×12·5. D–E, *Eophasmina manchesteri* gen. et sp. nov.; UF 15768–6315; D, ventral view; ×15. E, anterior (opercular) view; ×16·5.

Eophasmina manchesteri sp. nov.

Text-figures 4G–I, 5A–B, 7D–E

Derivation of name. For Dr Steven Manchester of the University of Florida.

Holotype. UF 15768–6316, middle Eocene, Nut Beds of the Clarno Formation, John Day Fossil Beds National Monument, north-central Oregon, USA. Paratypes: 15768–6314, 15768–6315, 15768–6317, 225–8688, all from the same horizon and locality.

Diagnosis. As for genus.

Dimensions. Capsule length 2·65–3·20 mm, width 1·35–1·50 mm, height 2·00–2·30 mm. Capsule volume 3·7–5·8 mm^3. Proportions: width/height 68–77 per cent; width/length 51–60 per cent; height/length 70–82 per cent.

DISCUSSION

Five small extinct families from the Triassic, Jurassic and Cretaceous, based mainly on wings, together with the extant Phasmatidae and Phylliidae have been attributed to the Phasmida by palaeontologists (Carpenter *in* Kaesler 1992), but entomologists employ a different classification,

scope and nomenclature for extant families. The latter is followed here, and the new taxa are included in the Pseudophasmatidae, tribe Anisomorphini, divisions not used by Carpenter.

The oldest previously reported evidence of 'Phasmatidae' *sensu* Carpenter is from the late Eocene (Ross and Jarzembowski 1993). Another early 'phasmatid' (in the palaeontological sense), *Agathamera reclusa* (Scudder), from sediments of probable Miocene age at Florissant, Colorado, USA, is a member of the Anisomorphini. Since the eggs described in the present paper are of middle Eocene age, they would appear to be the earliest record of one of the extant taxa. Nothing is known of the nature of eggs of the extinct families but there is great variation in egg morphology in Recent species, and there is a striking similarity between eggs of *Eophasma* to those of the Anisomorphini. All known eggs of this tribe are non-capitulate and have a marked negative opercular angle, similar to *Eophasma*. The *Anisomorpha* egg similarly also has a small micropylar plate with a distinct median line. The eggs of extant *Agathamera* Stål species have a micropylar plate that runs almost the full length of the capsule and there is no external median line. On balance, I suggest that the evidence supports allocating *Eophasma* to the Anisomorphini.

The eggs of *Eophasma* are clearly non-capitulate (i.e. do not carry a separate structure, a capitulum raised from the operculum). This appears to be a primitive condition, as does the general shape of the egg and the nature of the micropylar plate. In *Eophasmina*, it is possible that the central opercular cone did carry a capitulum, as such cones often do in the eggs of living species. If so, it might indicate that the link between ants and phasmid egg dispersal had developed already by the Eocene. On the other hand, the extant genus *Tectarchus* Salmon of the tribe Hemipachymorphini is unusual in having an egg with a central shallow opercular cone without a capitulum, and it also has a negative opercular angle. Therefore, the existence of a capitulum in *Eophasmina* is not proven. It is believed that the similarity between *Tectarchus* and *Eophasmina* is only superficial, and the latter may be a member of the Anisomorphini.

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