Late Eocene snakes from the Headon Hill Formation, southern England

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A number of Late Eocene, non-marine, microfaunal sites from the Headon Hill Formation in southern England have produced an unexpectedly diverse snake fauna. Well documented taxa include: *Paraplatyspondylia batesi, Totlandophis thomasae, Hordleophis balconae, Palaeopython cadurcensis, Paleryx rhombifer, Caduceryx pearchi* sp. nov., cf. *Calamagras* sp., cf. *Dunnophis* sp., *Headonophis harrisoni, Vectophis wardi* and *Russellophis tenuis*. Other snake taxa, reported in a preliminary way by previous authors are very doubtful elements in the fauna. These include: *Eoanilius* cf. *E. europae, Cadurcoboa* sp., cf. *Bransateryx, Platyspondylia* sp. and acrochordid sp. The well-documented snake taxa reinforce the concept that southern England, in Late Eocene times, had a fauna that differed somewhat from that of southwestern France. This is based on the greater diversity of the English fauna as well as other factors; including the presence of three distinct genera of caenophidian (advanced) snakes approaching the colubrid level (modern level) of snake evolution in the Late Eocene of southern England and only one such genus in the Late Eocene of southwestern France, and the several autochthonous Late Eocene English snake taxa that are absent in the Late Eocene of southwestern France.

KEY WORDS: Late Eocene, Snake, microvertebrates, Headon Hill Formation, England, diversity.

Introduction

Intensive microvertebrate collecting in the non-marine Late Eocene Headon Hill Formation of southern England from the late 1980's to the present, coupled with the availability of an automated sieving machine (Ward, 1981), a boon to the efficient breakdown of resistant fossil-bearing sediments, has provided a large number of snake fossils that supplement previous preliminary studies of fossil snakes in the formation. The new studies have demonstrated that a surprisingly diverse snake fauna existed in the area in the Late Eocene. During the 1990's and from 2001 to the present, D.L. Harrison and his field parties from the Harrison Institute (formerly Harrison Zoological Museum) collected microvertebrate fossils from several Late Eocene localities in the Headon Hill Formation in southern coastal England. Fossil-bearing matrix from these localities was processed at the Harrison Institute in the Ward sieving apparatus, prior to hand-picking the fossils from the concentrated matrix. This process has yielded the new material of fossil snakes presented in this paper, all of which is deposited in the Michigan State University Museum Vertebrate Paleontology Collection (MSUVP).

Localities and stratigraphy

The Late Eocene (Headon Hill Formation) localities referred to in the present paper are Hordle on the mainland, and Headon Hill, Totland Bay and Fishbourne on the Isle of Wight. For a recent account of British Tertiary stratigraphy see Daley & Balson (1999).

Hordle — The Late Eocene beds of Hordle Cliff, near Lymington, Hampshire contain three well-documented vertebrate strata (Cray, 1973; Benton & Spencer, 1995: 291), the Mammal, Crocodile, and Rodent beds. They all lie within the Totland Bay Member of the Headon Hill Formation of Insole & Daley (1985) (formerly "Lower Headon beds"). They are in European Land Mammal Age Zone MP17 and considered to be 39.5- 36 Ma (approximately) by Hooker (1989). The Rodent bed is considered to be about 0.75 Ma younger than the Mammal and Crocodile beds. All of these beds are composed of black lignitic to grey shelly clays and sandy silts. Snakes discussed here are either from the Mammal or Rodent beds.
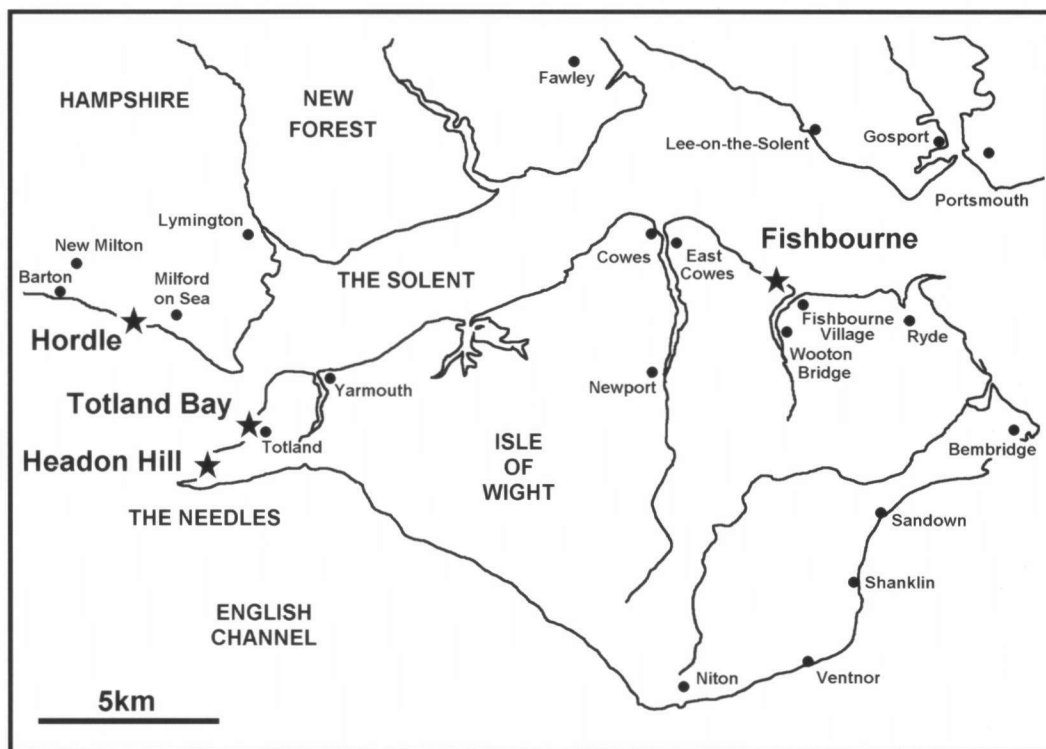
Figure 1. Map of the Isle of Wight and adjacent mainland, showing the localities cited in the text.

The Isle of Wight — Isle of Wight localities that have produced fossil snakes discussed in this paper consist of three sites. These are (1) the SW Headon Hill, (2) Totland Bay, and (3) Fishbourne. For the latest comprehensive account on Palaeogene sections in the Isle of Wight see Daley (1999). The SW Headon Hill locality (HH2 of Bosma (1974: 23-25) and referred to by Rage & Ford, 1980) is on the western half of the Isle, in the cliffs east of Hatherwood Point, near "The Needles" landmark. Vertebrate bones, including snakes, come from Late Eocene shelly lignitic clays immediately beneath the How Ledge Limestone. The locality is in the Totland Bay Member of the Headon Hill Formation (Insole & Daley, 1985) and equivalent in age to the Hordle Rodent Bed on the mainland.

The Totland Bay locality, TB of Bosma (1974: 27), also on the western part of the Island, is the same stratigraphic horizon as SW Headon Hill (above). It occurs below the How Ledge Limestone which outcrops in the cliffs in the northern part of the bay.

The Fishbourne locality is in the north-eastern part of the Island on the coast approximately 1 km NW of the village of Fishbourne between King's Quay and Wooton Creek. The vertebrates are found in lenticular bone beds in green and grey shelly muds. They are situated within the Fishbourne Member of the Headon Hill Formation and are higher in the section (Daley, 1999, text-fig. 3) than all of the localities of

this paper and is within mammal zone MP19 (Gale *et al.*, 2005).

Ordnance Survey (UK) Grid references of the cited localities —
Hordle Mammal Bed SZ 265 922
Hordle Rodent Bed SZ 2701 9205
SW Headon Hill (HH2) SZ 3055 8577 to 3060 8565
Totland Bay (TB) SZ 323 872
Fishbourne SZ 5519 937

Systematic palaeontology

Unfortunately, snakes reported from the Late Eocene Headon Hill Formation of England, other than those recently collected and reported here, have not been given museum numbers (Milner *et al.*, 1982; Milner, 1986) with the exception of those figured by Rage & Ford (1980). All measurements are in millimeters (mm). Following the modern rise of phylogenetic systematics ("cladistics"), snake taxonomy (as in many other vertebrate groups) is going through a phase of instability. McDiarmid *et al.* (1999) was adapted as the standard reference to snake nomenclature at the 10th Meeting of CITES 9-20 June, 1997. McDiarmid *et al.* (1999) employed a somewhat artificial system to recognize taxonomic catego-

ries above the family level in the hope that a classification will emerge that better reflects the phylogenetic relationships of snakes. A detailed discussion of the taxonomic history of each of the snake families and subfamilies that we follow here may be found in McDiarmid *et al.* (1999). Table 1 provides a systematic checklist of the Eocene snakes of the Headon Hill Formation.

ALETHINOPHIDIA
    Family Aniliidae
        ?Eoanilius cf. *E. europae*
MACROSTOMATA
    Family Boidae
        Subfamily indet.
            ?Cadurcoboa sp.
            Paraplatyspondylia batesi
            Totlandophis thomasae
        Subfamily Boinae
            Hordleophis balconae
            Palaeopython cadurcensis
            Paleryx rhombifer
        Subfamily Erycinae
            ?cf. Bransateryx sp.
            Cadurceryx pearchi n. sp.
            cf. *Calamagras* sp.
    Family Tropidopheidae
        cf. *Dunnophis* sp.
        Platyspondylia
CAENOPHIDIA
    Family *incertae sedis*
        Headonophis harrisoni
        Vectophis wardi
    Family Acrochordidae
        ? Acrochordid
    Family Russellopheidae
        Russellophis tenuis

Table 1. Checklist of Late Eocene Snakes of the Headon Hill Formation. Very doubtful species in this list are preceded by a "?".

Family Aniliidae

Remarks — This family consists of very primitive snakes. Living species are known from South America and the Indo-Malayan region. The Palaeogene forms are very small.

Genus *Eoanilius* Rage, 1974

Remarks — *Eoanilius* was described on the basis of about forty vertebrae (three illustrated) and a quadrate from the Late Eocene Phosphorites du Quercy of France (Rage, 1974). The nominate species, *Eoanilius europae* Rage, 1974 is known only from the Late Eocene. A second species, *E. oligocenicus* Szyndlar, 1994, is known from the Middle and Late Oligocene of Herrlingen 8, in Germany.

?*Eoanilius* cf. *E. europae* Rage, 1974

Remarks — *Eoanilius* cf. *E. europae* was reported in England on the basis of a single vertebra from the Late Eocene Mammal Bed of Hordle Cliff, Hampshire, by Milner *et al.* (1982). This taxon was not included in the later report on Palaeogene squamates from England by Milner (1986). Szyndlar (1994) again cited the Milner *et al.* (1982) record of this taxon. We were unable to assign any of the new snake material from the newly collected English Eocene material to *Eoanilius*. This record was also considered questionable by Rage & Augé (1993).

Family Boidae

Remarks — This family of rather primitive snakes consists of constricting species that range from small taxa to the giant snakes that occur in tropical areas today. They mainly occur in tropical and warm temperate areas.

Subfamily indeterminate
Genus *Cadurcoboa* Rage, 1978

Remarks — The genus *Cadurcoboa* is represented by a single species, *C. insolita*, that was described from the Late Eocene of the Phosphorites du Quercy in France. The combination of a depressed neural arch associated with a high neural spine in *Cadurcoboa* is very unusual in the Boidae (Rage, 1984). The lack of unspecialized caudal vertebrae in this taxon indicates that this genus does not belong in the subfamily Erycinae. Rage (1984) includes it as an indeterminate subfamily of the family Boidae.

?*Cadurcoboa* sp.

Remarks — "*Cadurcoboa* sp." was included without comment in the text in a list of squamates from the Late Eocene Hordle Mammal Bed (Milner *et al.*, 1982) and also without comment in the Late Eocene "Lower Headon Beds"= Totland Bay Member of the Headon Hill Formation by Milner (1986) of England. We have not found this genus in our studies. It seems probable that the material identified as *Cadurcoboa* actually represents the following genus, *Paraplatyspondylia*, or the diminutive boid genus *Hordleophis* that follows in the Boidae section.

Genus *Paraplatyspondylia* Holman & Harrison, 1998a

Remarks — The generic name refers to the fact that the taxon is morphologically similar to but not directly ancestral to the Late Eocene *Platyspondylia* Rage, 1974. *Paraplatyspondylia* was described from the Hordle Mammal and the Rodent beds and consists of a single species, *Paraplatyspondylia batesi*. *Paraplatyspondylia* shares the flattened vertebral arch condition as well as several other characters with *Platyspondylia*.

However, *Paraplatyspondylia* differs from *Platyspondylia lepta* Rage, 1974, in having a lower, longer neural spine that extends onto the base of the zygosphene and from both *P. lepta* and *P. sudrei* Rage, 1988 in the more anteriorly constricted neural spine, the truncated free edges of the prezygapophyses, and the deep cavities on either side of the cotyle. Turning to a comparison of *Paraplatyspondylia* with other, somewhat similar, boid genera, *Geringophis* Holman of the North American Oligocene and Miocene has a depressed neural arch, but its neural spine is higher than long and it has more distinct prezygapophyseal accessory processes than *Paraplatyspondylia* (as well as *Platyspondylia*). *Cadurcoboa* Rage also has a depressed neural arch, but it has a much higher neural spine and much stronger subcentral ridges than *Paraplatyspondylia* and *Platyspondylia*. We consider *Paraplatyspondylia* to represent an indeterminate subfamily of the family Boidae. Rage & Augé (1993) include *Platyspondylia* with the Tropidopheidae.

Paraplatyspondylia batesi Holman & Harrison, 1998

Material — The type material of *Paraplatyspondylia batesi* consisted of the holotype middle trunk vertebra (MSUVP 1434) from the Rodent Bed at Hordle Cliff; nineteen paratype trunk vertebrae (MSUVP 1435-1453) from the Rodent Bed. Additional (non type series) material; four trunk vertebrae (MSUVP 1454-1457) from the Hordle Mammal Bed. Material recently identified from the Hordle Rodent Bed consists of four middle trunk vertebrae (all under MSUVP 2060).

Genus *Platyspondylia* Rage, 1974

?*Platyspondylia* sp.

Remarks — "*Platyspondylia* sp." was included without comment in the list of squamates from the Late Eocene Hordle Mammal (Milner, *et al.,* 1982); and it was also included without comment, from the Late Eocene "Lower Headon Beds" of England (Milner, 1986). It is highly probable that this material actually represents *Paraplatyspondylia*.

Genus *Totlandophis* Holman & Harrison, 1998b

Remarks — The generic name refers to the Totland Bay Member of the Headon Hill Formation where the type material was collected. The monotypic genus *Totlandophis* is a small boid snake that differs from other boid genera in having an apparently unique upraised zygosphene, as well as other salient characters including: a moderately depressed neural arch; a posteriorly thickened neural spine that is somewhat longer than high and has an overhanging posterior edge. The prezygapophyseal and postzygapophyseal articular facets are well-developed with truncated leading edges. The prezygapophyseal accessory processes are very reduced.

Shallow depressions are on either side of the cotyle. There is a thick, strongly produced haemal keel and there are robust subcentral ridges.

Based on the suite of characters that separates *Totlandophis* from other related genera (especially the apparently unique upraised zygosphene), it would appear that the genus is an archaic boid taxon that did not survive beyond the Eocene and may not have any particularly close living relatives. It does not appear to represent the subfamily Boinae because of (1) having a more depressed neural arch, (2) having the odd upraised zygosphene, and (3) lacking the massive structure of the zygosphene and synapophyses. The rather small size and moderately flattened neural arch suggest that the affinities of *Totlandophis* could be with the subfamily Erycinae, but until caudal vertebrae are found, it cannot be assigned to this family with certainty. The function of the upraised zygosphene is unknown.

Totlandophis thomasae Holman & Harrison, 1998b

Material — The type material of *Totlandophis thomasae* consists of a single trunk vertebra (MSUVP 1458) from the Hordle Rodent Bed. Additional (non type series) material; 17 paratypes; vertebrae (MSUVP 1459-1475) from the Rodent Bed. No new material has been identified.

Subfamily Boinae

Remarks — The snakes of this family are generally medium to large-sized constricting snakes that presently are tropicopolitan or live in warm, temperate areas. Some of the early Tertiary forms, however, are quite small.

Genus *Hordleophis* Holman, 1996

Remarks — The genus *Hordleophis* represents a truly diminutive member of the subfamily Boinae to which it is assigned on the basis of having (1) the neural arch not flattened and not elaborated by additional processes, (2) the prezygapophyseal accessory processes reduced but not absent; (3) the neural spine high and very well-developed. Other characters include prezygapophyses oriented anterolaterally; undivided synapophyses; deep paracotylar depressions that lack paracotylar foramina. The haemal keel has deep grooves. This boid genus differs from the European Tertiary Boinae genera *Palaeopython* and *Paleryx* in its diminutive size and higher, rounded neural spine; as well as in its deeper paracotylar depressions and less laterally oriented zygapophyses. *Hordleophis* resembles the Boidae *incertae sedis* genus *Cadurcoboa* in its high, anteriorly rounded neural spine and moderately vaulted neural arch. It differs from *Cadurcoboa* on the basis that its neural spine is both anteriorly and posteriorly rounded and dorsally unswollen; that its prezygapophyseal accessory processes are very weakly developed; and in that it has a wider haemal keel. Since *Hordleophis* has no known fossil or living close relatives, it probably was a

dead-end form.

Hordleophis balconae Holman, 1996

Material — The type material of *Hordleophis balconae* consists of a holotype trunk vertebra (MSUVP 1361) from the Hordle Rodent Bed and three paratype trunk vertebrae (MSUVP 1362-1364) also from the Hordle Rodent Bed. No new material has been designated.

Genus *Palaeopython* Rochebrune, 1880

Remarks — The genus *Palaeopython* was originally described from un-named localities in the Late Eocene "Phosphorites du Quercy", France and also occurs in the Middle Eocene of France and possibly the Late Eocene of Switzerland (Rage, 1984). The boine genera *Palaeopython* and *Paleryx* Owen, 1850 were synonymised by Lydekker (1888a, b), but Rage (1984) pointed out that they are distinct. *Palaeopython* has a wider vertebra than *Paleryx* with a more robust zygosphene that is wider than the cotyle. Moreover, the synapophyses of the anterior trunk vertebrae are less distinct from the centrum and less slanted than in *Paleryx* (Rage, 1984). Both of these genera represent moderately large snakes that undoubtedly killed their prey by constriction.

Palaeopython cadurcensis (Filhol, 1877)

Remarks — *Palaeopython cadurcensis* has a more vaulted neural arch that distinguishes it from the other three named species in the genus, each of which is based on vertebrae (Rage, 1984). *Palaeopython cadurcensis* has never been reported from Britain, although *Palaeopython* sp. was reported from the "Lower Headon Beds" of the Hampshire, England (Milner, 1986). *Palaeopython cadurcensis* was originally described from un-named localities in the Middle to Late Eocene "Phosphorites du Quercy", France; and also occurs in the Middle Eocene of France. Remains of *Palaeopython* sp. and *Palaeopython* cf. *filholi* have been found in the Late Eocene of Switzerland (Rage, 1984).

New material — Two anterior trunk vertebrae (MSUVP 2051-2052) and a middle trunk vertebra (MSUVP 2053) from the Hordle Rodent Bed and a middle trunk vertebra (MSUVP 2058) from the Hordle Mammal Bed.

Description of the new material — All of the four vertebrae are distinctly wider than long and have the vaulted neural arches typical of *Palaeopython cadurcensis*. The three vertebrae with both the zygosphene and the cotyle present are anterior trunk vertebra MSUVP 2051 and middle trunk vertebrae MSUVP 2053 and 2058. MSUVP 2051 has the width of the zygosphene 5.5 mm and the width of the cotyle 4.8 mm, MSUVP 2053 has the width of the zygosphene 4.2 mm and the width of the cotyle 3.8 mm, and MSUVP 2058 has the width of the zygosphene 3.4 mm and the width of the

cotyle 2.8 mm. The haemal keel is narrow in the two anterior trunk vertebrae and relatively wide in the two middle trunk vertebrae. The height of the largest vertebra (MSUVP 2051) from the top of the neural spine through the condyle is 13.8 mm. The same height in the smallest vertebra (MSUVP 2058) is 6.8 mm. The largest vertebra (MSUVP 2051) represents a snake roughly of 1.25 meters in total length.

Genus *Paleryx* Owen, 1850

Remarks — *Paleryx rhombifer*, the only recognized species of the genus, was originally described from Hordle Cliff by Owen in 1850. It is known only on the basis of vertebrae from this locality. Owen (1850) originally described two species from Hordle Cliff, *Paleryx rhombifer* and *P. depressus*. Rage (1984) attributed the differences between these two taxa to intracolumnar variation as the type specimen of *P. rhombifer* is an anterior vertebra and the syntypes of *P. depressus* are posterior or middle trunk vertebra and relegated *P. depressus* to the synonymy of *P. rhombifer*.

Paleryx rhombifer Owen, 1850

Material — Rage & Ford (1980) assigned "About twenty more or less fragmentary trunk vertebrae...." from the Headon Hill Locality of the Isle of Wight to *Paleryx rhombifer* and a rounded and worn trunk vertebra from Fishbourne, Isle of Wight to *Paleryx*, stating that it probably belongs to *P. rhombifer*. Milner *et al.* (1982) listed *P. rhombifer* from the Hordle Mammal Bed and Milner (1986) included this taxon in her list of snakes from the "Lower Headon Beds" of England.

Subfamily Erycinae

Remarks — This subfamily of small boid snakes are fossorial and burrow in sandy soils. At present, most of them are tropicopolitan or live in warm temperate regions. These snakes have compressed vertebrae in the posterior part of the caudal portion of the vertebral column. These vertebrae are swollen to a greater or lesser degree and sometimes have extra vertebral processes such as pterapophyses. Sometimes these vertebrae are elaborated to a remarkable extent.

Genus *Bransateryx* Hoffstetter & Rage, 1972

Remarks — This genus has very elaborated caudal vertebrae with extra processes on them. This genus was first described from the Late Oligocene of Coderet, Allier, France (Rage, 1984). The genus is known only in Western Europe where it occurs from the Early Oligocene to the Early Miocene. A single species, *Bransateryx vireti* Hoffstetter & Rage, 1972 is known.
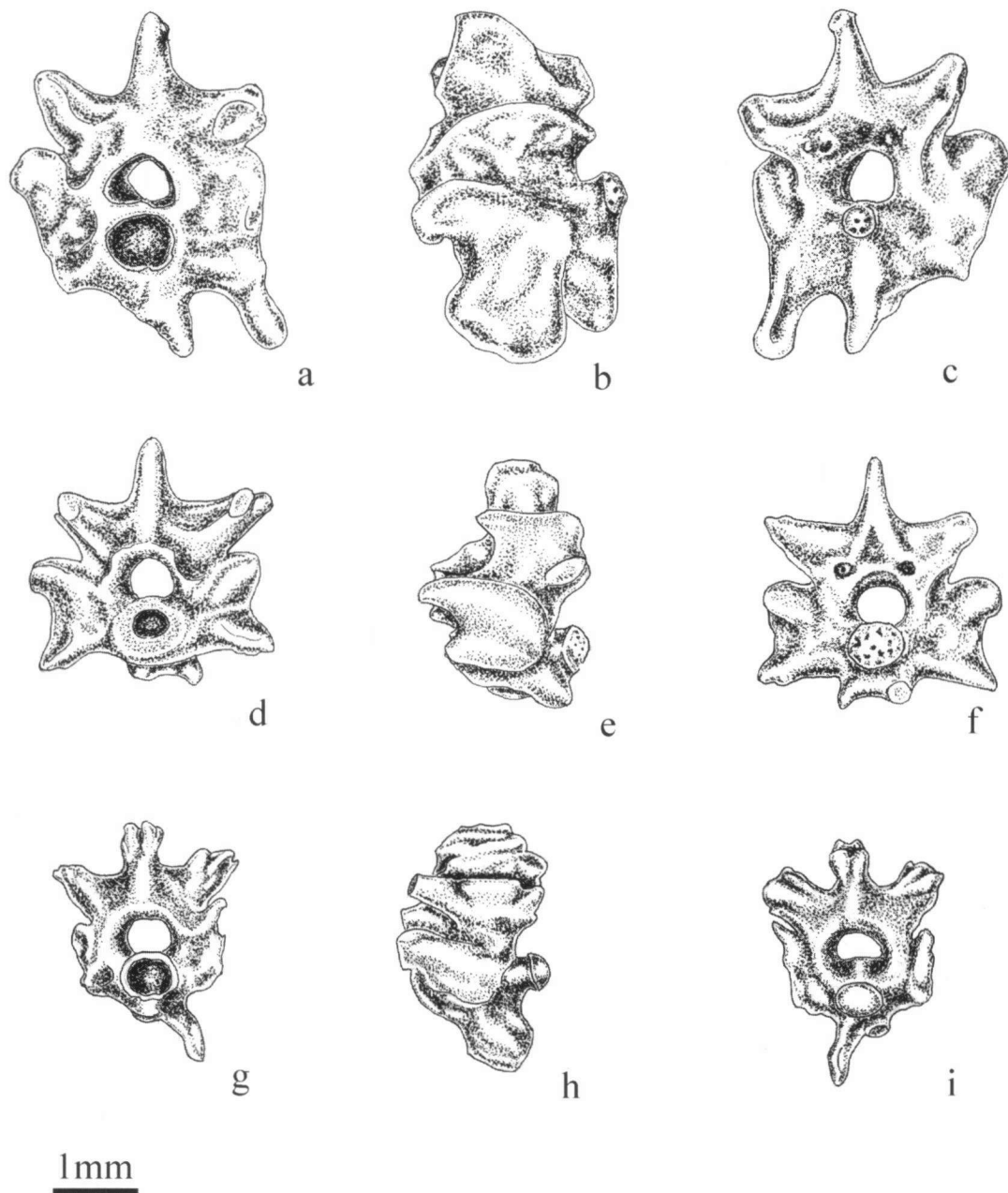
Figure 2. Snake vertebrae from the Late Eocene Rodent Bed at Hordle, Hampshire England.
a-c. Caudal vertebrae of *Cadurceryx pearchi* sp. nov., noiotype, (MSUVP 2061); a, anterior view; b, left lateral view; c, posterior view.
d-f. Caudal vertebrae of *Cadurceryx pearchi* sp. nov., paratype, (MSUVP 2062); d, anterior view; e, left lateral view; f, posterior view.
g-i. Caudal vertebrae of *Cadurceryx pearchi* sp. nov., paratype (MSUVP 2059): g, anterior view; h, left lateral view; i, posterior view.
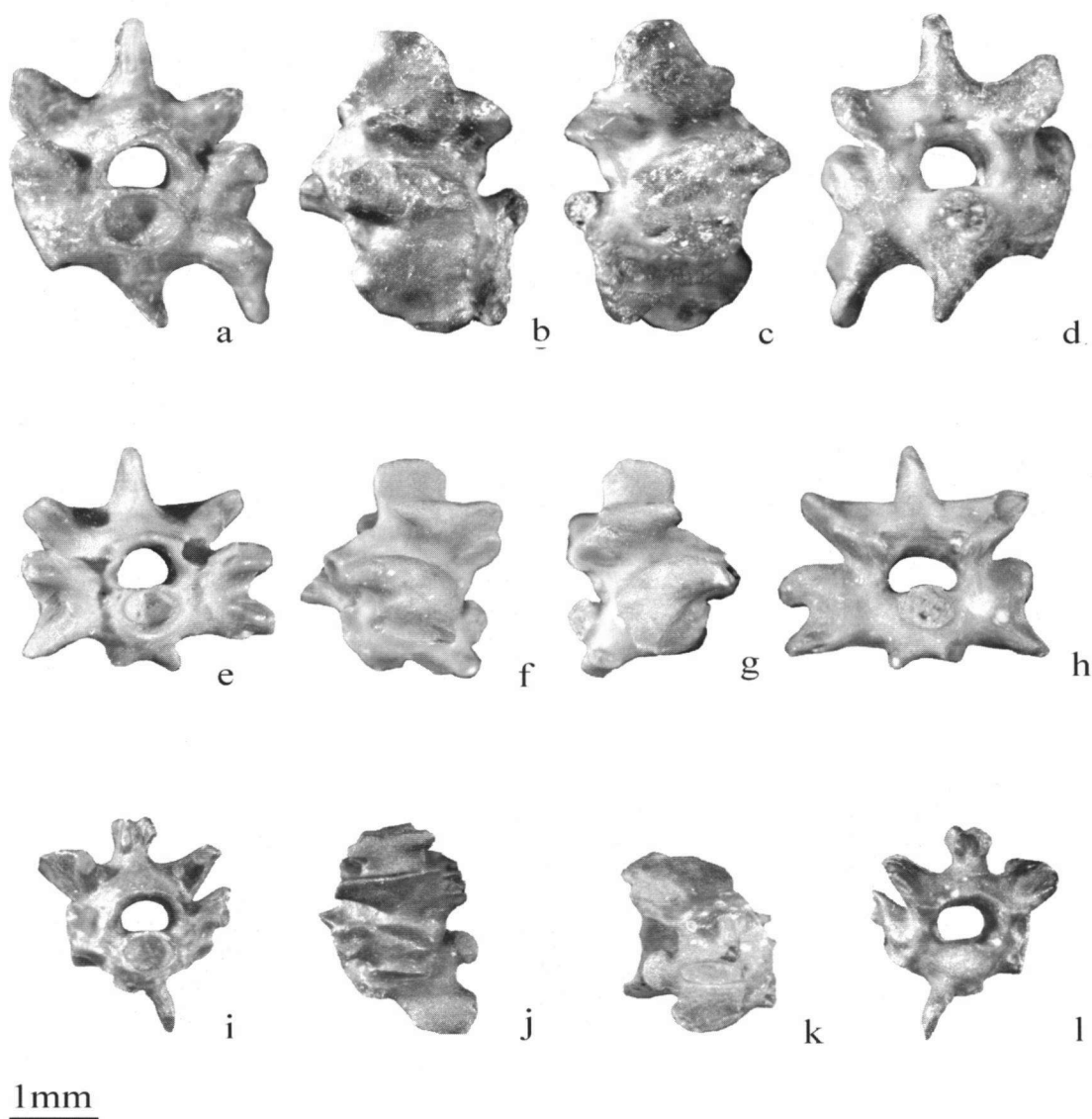Scale bar 1 mm.

Figure 3. Snake vertebrae from the Late Eocene Rodent Bed at Hordle, Hampshire England.

a-d. Caudal vertebrae of *Cadurceryx pearchi* sp. nov., holotype (MSUVP 2061): a, anterior view; b, left lateral view; c, right lateral view; d, posterior view.

e-h. Caudal vertebrae of *Cadurceryx pearchi* sp. nov., paratype (MSUVP 2062): e, anterior view; f, left lateral view; g, right lateral view; h, posterior view.

i-l. Caudal vertebrae of *Pterygoboa* sp. indet. (MSUVP 2059): i, anterior view; j, left lateral view; k, right lateral view; l, posterior view.
Scale bar 1 mm.

? cf. Bransateryx

Remarks — A record of cf. *Bransateryx* was listed by Milner (1986) from the "Lower Headon Beds" of the Late Eocene of England, but was not discussed in the text and is questionable. This genus was not listed by previous authors (Milner *et al.*, 1982; Rage & Ford, 1980) and we have not found it among the snakes we have recently studied from the Headon Hill Formation.

Genus *Cadurceryx* Hoffstetter & Rage, 1972

Remarks — This genus was formerly composed of a single species, *Cadurceryx filholi* Hoffstetter & Rage, 1972 from an unknown Late Eocene locality of the "Phosphorites du Quercy", France. The very distinctive caudal vertebra of the genus was figured by Rage (1984). *Cadurceryx* has been reported from the Middle and Late Eocene of France (Rage, 1984) and from the "Lower Headon Beds" of the Late Eocene of England (Milner, 1986). The record from England was reported as *Cadurceryx* sp. *Cadurceryx* is another taxon with the posterior vertebrae elaborated with extra processes, but not as many as in *Bransateryx*.

Cadurceryx pearchi sp. nov.
Fig. 2, a-f; Fig 3, a-h.

Type material — holotype: A single caudal vertebra, Michigan State University Museum Vertebrate Paleontology No. MSUVP 2061 (Fig 2 a-c; Fig 3, a-d); paratypes: four caudal vertebrae, MSUVP 2062 (Fig. 2, d-f; fig. 3 e-h). MSUVP 2059, 2063-2064 from the same locality and horizon as the holotype.

Type locality and horizon — The Rodent Bed, Hordle, Hampshire, England, Totland Bay Member of the Headon Hill Formation (Late Eocene).

Etymology — The name recognizes the contribution to British Eocene palaeontology of Malcolm Pearch, of the Harrison Institute, Sevenoaks, Kent.

Diagnosis — Caudal vertebrae that differ from those of *Cadurceryx filholi* Hoffstetter & Rage in having: (1) cotyle larger than neural canal (cotyle smaller than neural canal in *P. filholi*); (2) anterior ends of prezygapophyses produced as a knoblike tubercle (not so in *C. filholi*).

Measurements — Holotype MSUVP 2061: Height (tip of neural spine to basal extent of the haemapophyses): 4.03 mm. Width (maximum separation of the pleurapophyses) *estimated, (as the right pleurapophysis is absent): *3.19 mm. Length (cotyle to condyle): 2.21 mm; paratype: MSUVP 2062 Height: 2.94 mm; width: 2.86 mm, length: 1.72 mm.

Description of the holotype with reference to Cadurceryx

filholi — In anterior view, in both *C. pearchi* and *C. filholi*, the neural spine is moderately wide at its base and tapers dorsally to a rounded point, rather than being swollen as in some other Erycinae genera (see Rage, 1984). The neural spine is also not terminally bifid in either *C. pearchi* or *C. filholi* as in some other erycine genera (also see Rage, 1984). In *C. pearchi* the neural spine is much higher than the greatest height of the neural canal, but in *C. filholi* it is not as high as the greatest height of the neural canal. The pterapophyses are moderately tilted upward in anterior view in *C. pearchi*, but only slightly tilted upward in *C. filholi*. Continuing to observe the vertebrae anteriorly, the neural canal is roughly triangular in shape in *C. pearchi*, whereas it is oval in shape and slightly depressed in *C. filholi*. The anterior ends of the prezygapophyses are produced as knoblike tubercles in *C. pearchi*, but these tubercles do not occur on the anterior ends of the prezygapophyses in *C. filholi*. The cotyle is round in *C. pearchi*, but is a very slightly depressed oval in *C. filholi*. Somewhat knoblike projections occur on the anterior ends of the pleurapophyses in *C. pearchi* and *C. filholi*, but they are rotated more anteriorly in *C. pearchi*. The pleurapophysis that is present in *C. pearchi* is about as long (low) as the haemapophyses, but in *C. filholi* the pleurapophyses are only about half as long as the haemapophyses. In lateral view, the neural spine is about as long as it is high in both species, but it is not as constricted at its base in *C. pearchi* as it is in *C. filholi*. In this view, the pterapophyses are directed more anteroventrally in *C. pearchi* than in *C. filholi*. The prezygapophyses are directed slightly upward in both species. The pleurapophyses are very wide in both species in lateral view, but the anterior border of this structure is convex in *C. pearchi* and concave in *C. filholi*. In posterior view, the pterapophyses are even more sharply tilted upward in *C. pearchi* compared with *C. filholi* than they are in anterior view.

Description of the paratypes — The four paratypes show no trenchant differences from that of the holotype and are remarkably similar to the holotype. MSUVP 2064 is the least complete of the four caudal vertebrae in the type series in that the neural spine is broken off about two-thirds from its apex. The cotyle is somewhat smaller in relation to the neural canal in MSUVP 2064 than in the other three *Caduceryx pearchi* caudal vertebrae.

Genus *Calamagras* Cope, 1873

Remarks — The genus *Calamagras* occurs in the Eocene and Oligocene of North America, the Early Eocene of France and the Late Eocene of England. The French *Calamagras* consists of a single species, *Calamagras gallicus* Rage, 1977.

cf. Calamagras sp.

Remarks — Rage & Ford (1980) reported cf. *Calamagras* from the Fishbourne locality. Milner *et al.* (1982) listed

Calamagras species from the Hordle Mammal Bed; and Milner (1986) listed cf. *Calamagras* from the "Lower Headon Beds".

Family Tropidopheidae

Remarks — Modern snakes of this family occur in the New World tropics and are mainly of small size. Fossil forms of this family of the extinct genus *Dunnophis* have been found in the Eocene (and possibly the Palaeocene) of the western United States and in the Eocene of France (Rage, 1984).

Genus *Dunnophis* Hecht, 1959

Remarks — Three species of this genus are presently recognized. *Dunnophis microechinus* Hecht is known from the Early Eocene of Wyoming (Holman, 2000), *Dunnophis matronensis* Rage is known from the Early Eocene of France and *Dunnophis cadurcensis* Rage is known from the Late Eocene of France.

cf. *Dunnophis* sp.

Remarks — Rage & Ford (1980) discussed "less than ten vertebrae, only one in good condition" from the Late Eocene of Fishbourne, Isle of Wight, that they tentatively identified as cf. *Dunnophis*, remarking that the specimens showed some differences from the genus, including a sharp haemal keel on the trunk vertebrae. Milner *et al.* (1982) identified vertebrae from the Hordle Mammal Bed as cf. *Dunnophis*, remarking that these possessed a distinct haemal keel, not known in other *Dunnophis* material. Milner (1986) listed *Dunnophis* sp. from the "Lower Headon Beds" without comment.

Family Acrochordidae

Remarks — This group is composed of a single living aquatic genus, *Acrochordus* that occurs from India to Australia and the Solomon Islands. It has rather boid-like vertebrae and the other a more lightly built vertebrae are not particularly boid like. It has hypapophyses throughout the vertebral column and lacks pelvic vestiges, characters not found in boids. *Acrochordus* is known from the Middle Miocene of Pakistan (Rage, 1984).

?Acrochordid species and genus indet.

Remarks — Milner (1986) lists, without comment, "Acrochordid" on the basis of apparently a single vertebra from the "Lower Headon Beds" of England. This record is very questionable.

Family Indeterminate
Genus *Headonophis* Holman, 1993

Remarks — The colubroid genus *Headonophis* was described by Holman (1993) on the basis of a single trunk vertebra (MSUVP- 1342) [this vertebra not identified as to its position on the column by Holman, 1993] from Late Eocene SW Headon Hill, Isle of Wight. Diagnostic features of the genus are a trunk vertebra with weak, narrow zygopophyses that are oriented much more anteroposteriorly than laterally; prezygapophyseal accessory processes absent; synapophyses undivided; paracotylar fossae well-developed with a distinct central foramen in each fossa; neural arch moderately flattened; and a low, massive, hypapophysis with a distinct foramen on either side, in the middle of its extent. Holman (1993) was unable to assign *Headonophis* to a specific caenophidian family, but pointed out that the genus has an elongate, lightly constructed vertebral form and a long neural spine as in caenophidians. *Headonophis* resembles the other odd colubroid families Anomalopheidae and Russellopheidae in having weak, narrow zygapophyses that are oriented much more anterolaterally than laterally, no apparent synapophyseal division (possibly indicating single articular rib facets), and no prezygapophyseal accessory processes. *Headonophis* shares three characters with the Russellopheidae that it does not share with the Anomalopheidae. These are: vertebrae more lightly constructed; large neural canal; and a less massive neural arch. On the other hand, *Headonophis* exhibits five characters that are distinct from both the Russellopheidae and the Anomalopheidae which are: a more flattened neural arch; more angular synapophyses; paracotylar foramina; a low, massive hypapophysis; and a distinct foramen on either side of the haemal keel. The genus *Headonophis* as well as the two following genera are considered primitive caenophidians.

Headonophis harrisoni Holman, 1993

New material — Four posterior vertebrae (i.e. cloacal or caudal vertebrae that occur behind the trunk region; see Holman, 2000, fig. 7, p. 12) including one caudal vertebra (MSUVP 2054) and three vertebrae (MSUVP 2055-2057) whose position in the posterior vertebral column cannot be verified. All of the four vertebrae are identified as posterior vertebrae on the basis of the presence of remnants of paired haemapophyses that occur on the posterior part of the bottom of the centrum. MSUVP 2054 is identified as a caudal vertebra on the basis of having a robust pleurapophysis on the right side of the centrum under the prezygapophysis. The pleurapophysis is broken off on the left side. Two of these posterior vertebrae (MSUVP 2055 and 2057) bear complete, rounded condyles that are situated at the end of long neck regions and extend well beyond the posterior end of the centrum. Complete condyles are not known in the other vertebrae of *Headonophis* including the holotype trunk vertebra. All of the four new vertebrae are elongate and lightly built and have weak zygapophyses that are oriented much more anteroposteriorly than laterally and many of the other diagnostic characters of the holotype are preserved. The four posterior vertebrae, not unexpectedly, are all smaller than the type trunk vertebra which had a length through the zyga-

pophyses of 3.8 mm. The greatest length through the zyga-pophyses of three of the posterior vertebrae are 3.0 mm (MSUVP 2054), 2.8 mm (MSUVP 2055), and 2.3 mm (MSUVP 2056). In MSUVP 2057, the greatest length through the cotyle and condyle is 2.2 mm.

Genus *Vectophis* Rage & Ford, 1980

Remarks — This odd genus is known only from the "Lower Headon Beds" of the Eocene of England.

Vectophis wardi Rage & Ford, 1980

Remarks — This snake has vertebrae that are lightly built as in the Caenophidia, but they are about as long as they are wide and have other characters indicating relationships to the Tropidopheidae and the Russellopheidae, another primitive colubroid group. We are rather ambivalent as to the relationships of this snake, which probably is a dead-end form. Nevertheless, the consensus of Milner *et al.* (1982) and Rage (1984) is that *Vectophis wardi* is a Caenophidia *incertae sedis* and thus we have placed *V. wardi* in this taxonomic position here. *Vectophis wardi* is known from Totland Bay, Isle of Wight (type locality of Rage & Ford, 1982) and has been reported from the Hordle Mammal Bed by Milner *et al.* (1982). Milner (1986) lists it from the "Lower Headon Beds" of England.

Family Russellopheidae

Remarks — This monotypic family is known on the basis of a single species, *Russellophis tenuis* from the Early Eocene of the Paris Basin of France. *Russellophis* sp. has been reported from the Middle/Late Eocene Creechbarrow Limestone and the Late Eocene Bembridge Limestone and "Lower Headon Beds" of England by Milner (1986) without comment.

Russellophis tenuis Rage, 1975

New material — One anterior trunk vertebra MSUVP 2065 from the Hordle Mammal Bed, Hampshire, England.

Remarks — We are unable to separate this single vertebra from that of *Russellophis tenuis*. The vertebrae of *R. tenuis* are elongate and lightly built with a vaulted neural arch. They differ from *Headonophis* in characters given in the *Headonophis* section above. *Russellophis* is thought to have been aquatic.

Discussion

The following discussion deals with two topics: (1) a taxonomic comparison of the snake fauna of the Late Eocene of

southern coastal England with that of the snake fauna of the Late Eocene Phosphorites du Quercy beds of southwestern France and (2) a discussion of the zoogeographical origins and immigration patterns of these faunas.

southern England	southwestern France
ANILIIDAE	
-	*Coniophis* sp.
-	*Eoanilius europae*
BOIDAE	
Boidae subfamily indet.	
-	*Cadurcoboa insolita*
Paraplatyspondylia batesi	-
Totlandophis thomasae	-
Boinae	
Hordleophis balconae	-
Palaeopython cadurcensis	*Palaeopython cadurcensis*
-	*Palaeopython filholi*
Paleryx rhombifer	-
Erycinae	
-	*Cadurceryx filholi*
Cadurceryx pearchi	-
cf. *Calamagras*	-
TROPIDOPHIIDAE	
cf. *Dunnophis*	*Dunnophis cadurcensis*
-	*Platyspondylia sudrei*
CAENOPHIDIA	
FAMILY INDET.	
Headonophis harrisoni	-
Vectophis wardi	-
RUSSELLOPHEIDAE	
Russellophis tenuis	russellopheid (?new genus)

Table 2. Late Eocene Snakes of southern England compared with those from the Late Eocene of southwestern France (doubtful [?] taxa omitted).

In this discussion, fossil snakes from the Late Eocene of England of doubtful status (those preceded by "?" in the text and tables) are omitted. One must remember that the stratigraphic range of the Eocene portion of the "Phosphorites de Quercy" is more extended than that of the English localities. It extends from middle Lutetian to the end of the Eocene, 46 Ma to 36-35 Ma (Harland *et al.*, 1990).

Relative to the number of snake taxa present, (Tables 2 and 3), 11 genera are present in the Late Eocene of southern England (SE) and at least 9 genera are present in the Late Eocene of southwestern France (SWF). Turning to generic similarity, only 3 genera are shared by both regions, these taxa all being in the macrostomate families Boidae and Tropidopheidae; namely *Palaeopython* (Boidae: Boinae), *Cadurceryx* (Boidae: Erycinae), and *Dunnophis* (Tropidopheidae). Only one species is the same in both regions, this species being the boid *Palaeopython cadurcensis* (Boidae: Boinae).

No uncontested snakes of the alethophidian family Aniliidae are present in SE, but two, *Coniophis* sp. and *Eoanilius europae* are present in SWF.

	S England	SW France
Total number of genera	11	9
Number of species identified	9	7
Number of the same genera	3	3
Number of the same species	1	1
Number of primitive genera (Aniliidae)	0	2
Number of boid genera	8	4
Number of caenophidian genera	3	1
Number of genera also occurring in the North American Tertiary	4	2

Table 3. Summary table of taxonomic similarities and differences between Late Eocene snakes of southern England (SE) and those of southwestern France (SWF) (very doubtful [?] taxa omitted).

On the other hand, only one caenophidian (advanced snakes), russellopheid (? new genus) is present in SWF; but three genera are present in SE, namely *Headonophis harrisoni, Vectophis wardi,* and *Russellophis tenuis.* These three genera have approached but have not reached the true colubrid stage of evolution (see Rage, 1984 and Holman, 1993). Relative to the number of genera in SE and SWF also occurring in North American Tertiary, four from SE occur there; namely *Totlandophis* (Boidae: subfamily indet.), cf. *Calamagras* (Boidae: Erycinae) and cf. *Dunnophis* (Tropidopheidae). However, only two genera in SWF (*Coniophis* sp. of the Aniliidae and *Dunnophis* of the Tropidopheidae) also occur in the North American Tertiary.

Turning to zoogeographic origins, the aniliids are thought to have migrated from South America through North America to Europe and then (hypothetically) to Asia (Rage, 1982). This movement was said to have begun in the Late Cretaceous. *Coniophis,* however, has since been found in the Middle Cretaceous of North America and Africa (see Holman, 2000; Rage & Werner, 1999), thus the movement obviously began earlier. Whether aniliids passed by SE in their Palaeogene movements, or whether the lack of remains of this primitive family in SE is a palaeontological sampling bias, is not known.

According to the model of Rage (1982), the Boidae and the Tropidopheidae (formerly considered a subfamily of the Boidae by Rage, 1984) had essentially the same immigration pattern as the Aniliidae, but there is no evidence that this immigration predated the Late Cretaceous. Boids and tropidopheids from SE following this pattern include *Paraplatyspondylia batesi* and *Totlandophis thomasae* (Boidae indet.); *Hordleophis balconae, Palaeopython cadurcensis,* and *Paleryx rhombifer* (Boinae); *Cadurceryx pearchi,* cf. *Calamagras* and cf. *Dunnophis* (Tropidopheidae).

The Caenophidia contains several poorly known families that approach but that do not fully reach the level of evolution of the modern snakes (Colubridae). The first Colubridae (modern snakes) are known in the Late Eocene at about the same time in North America (36.0-34.2 Ma; Georgia, USA) and in Thailand (ca 34.6-33.5 Ma) (Parmley & Holman, 2003; Rage *et al.,* 1992) and very colubrid-like snake vertebrae are

known from the Middle Cretaceous of Sudan (Rage & Werner, 1999).

Thus, one of the most interesting aspects of the SE and SWF snake fauna is the lack of true colubrid snakes in either one of them. On the other hand the SE has three genera of caenophidians that represent poorly known or unnamed families that approach, but do not fully reach the level of evolution of the Colubridae and SWF has only one. The age of both sites ranges from about 36 to 39 Ma, thus both localities may be slightly older than the North American and Thailand true colubrids. However, we might suggest another reason for the presence of the isolated caenophidian genera; and that is that each of these two regions were quite isolated, probably existing as large islands. The same reasoning could be applied to the autochthonous snake genera and the lack of aniliid snakes in SE and the presence of two genera of aniliids in SWF.

Acknowledgements

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