J.N.C.C.

Fossil Reptiles of Great Britain

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Chapter 9

British Caenozoic fossil reptile sites

INTRODUCTION: BRITISH CAENOZOIC STRATIGRAPHY AND SEDIMENTARY SETTING

The British Caenozoic is marked by extensive vulcanism in northern areas (especially Mull and the other Hebridean islands, and Northern Ireland), and by deposition of sediments in a number of basins in the North Sea, the English Channel and the southern Irish Sea. These offshore basins exhibit sections that correlate with onshore outcrops (Figure 9.1) on the Isle of Wight, in the Hampshire Basin and in the London Basin (northern Kent, London, Berkshire, Essex and extending up the coasts of Suffolk and Norfolk). The sediments are all Palaeogene (Palaeocene, Eocene, Oligocene, Figure 9.2) in age, except for a limited Neogene (Pliocene) sequence in Suffolk, and restricted Mio-Pliocene occurrences in Kent, Norfolk and Cornwall (Curry *et al.*, 1978). Younger Caenozoic sediments (Pleistocene, Holocene) are more abundant, being distributed over much of the British Isles and yielding fossil vertebrates especially in East Anglia and southern counties of England.

At the end of the Cretaceous much of Britain lay beneath the Chalk sea, but uplift was taking place. A large part of Britain became land during the Tertiary, with strongest uplift in the north and west, and renewed subsidence in the south-east.

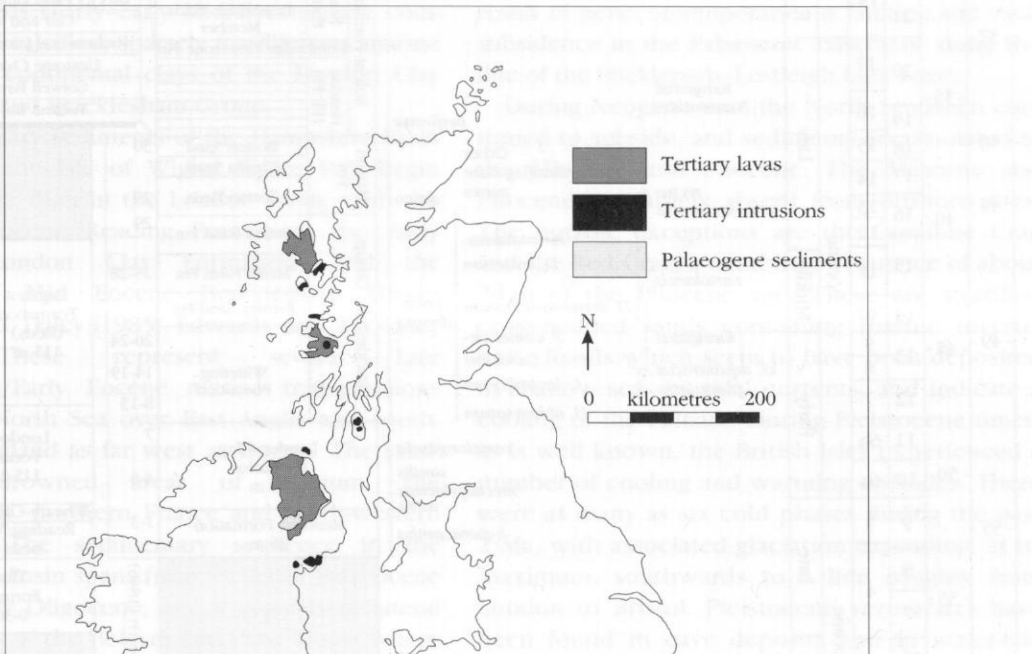

Figure 9.1 Map showing the distribution of Tertiary rocks in Great Britain. Only major divisions are indicated, and an enlargement of the Hampshire and Isle of Wight areas is given. GCR Tertiary reptile sites: (1) Warden Point; (2) Barton Cliff; (3) Hordle Cliff; (4) Headon Hill and Totland Bay; (5) Bouldnor and Hamstead Cliffs.

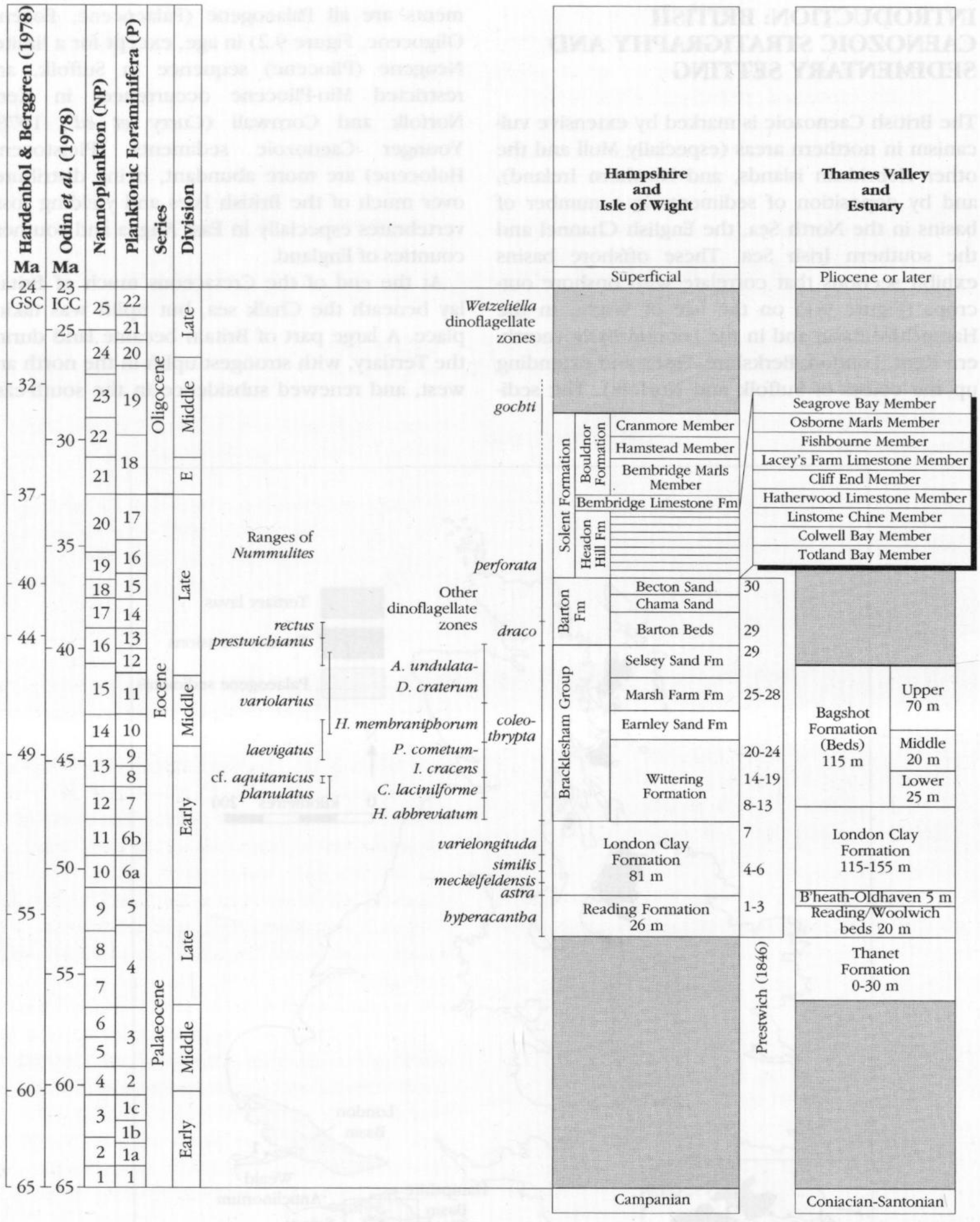

Figure 9.2 Summary of Tertiary stratigraphy, showing global standards and some major British formations. Based on Curry *et al.* (1978).

The sediments of the London and Hampshire Basins record the interplay of marine sediments from the subsiding basins and tongues of terrestrial sediments feeding off the lands to the north. This produces cyclic patterns recording repeated transgressions and regressions.

The earliest transgressive beds, of Late Palaeocene age, occur in eastern Kent (Thanet Formation), and these marine units extended ever further westwards through Berkshire and into

Wiltshire during the Late Palaeocene (Woolwich and Reading Beds) and Eocene (London Clay Formation, Bagshot beds). The Reading Formation (Late Palaeocene) is represented by a sequence of non-marine, red, mottled, kaolinitic clays and sands of fluvial origin that have yielded plant and insect fossils, as well as a marine horizon toward the base (Bone, 1986). The London Clay Formation (Early Eocene) is characterized by monotonous dark-grey to bluish mudstones, some of which are intensely bioturbated, together with more sandy beds near the base. The abundant fossils include diverse molluscs (bivalves, gastropods, nautiloids), crustaceans, fishes and tetrapods, and over 500 species of flowering plants (angiosperms) and gymnosperms, both groups being represented by pollen, logs, fruits and leaves. The Bagshot beds (Early–early Mid Eocene) are composed of decalcified, sparsely fossiliferous, marine sands and continental clays of the London Clay Formation and Bracklesham Group.

The Tertiary sediments of the Hampshire Basin (including the Isle of Wight; Figure 9.2) begin slightly later than in the London Basin, with the Late Palaeocene Reading Formation, the Early Eocene London Clay Formation, and the Early–early Mid Eocene Bracklesham Group (Insole and Daley 1985; Edwards and Freshney 1987). These represent several Late Palaeocene/Early Eocene marine transgressions from the North Sea over East Anglia and south-eastern England as far west as Dorset. The same episode drowned areas of Belgium, the Netherlands, northern France and north-western Germany. The sedimentary sequence in the Hampshire Basin spans from the latest Palaeocene to the Early Oligocene, and it consists of lateral equivalents of the Belgian and Paris basins where the sequences consist of limestones terrigenous clastics including sands, clays and thick deposits of lignite.

The Bracklesham Group includes a variety of marine and continental facies that appear to have been deposited over a long interval of time spanning the Early to early Mid Eocene. The marine units of the Group are restricted to the east of the outcrop, while in the Isle of Wight it is in part continental, and the commonest fossils are leaves and palynomorphs. The succeeding 'Barton Sands' and lower part of the Headon Hill Formation (Totland Bay Member; Late Eocene) are marine in the lower section and broadly continental toward the top. The upper parts of the Headon Hill Formation (Colwell Bay Member to Seagrove Bay Member; latest Eocene), and the Bembridge Limestone and Bouldnor formations (Early–Mid Oligocene), which is confined to the north of the Isle of Wight, consist of mainly continental facies, with rare marine-influenced units in the Cranmore Member of the Bouldnor Formation (Insole and Daley, 1985). This whole sequence, barring the 'Barton Sands' at the base, is placed in the Solent Group (Insole and Daley, 1985).

In Northern Ireland and the Inner Hebrides, rare Tertiary sediments include the eroded remnants of a vast Palaeogene region of plateau lavas (Tertiary Igneous Province), and some associated subsidiary continental sedimentary deposits. In south-west England the Oligocene basins of Bovey and Petrockstow contain fluvially deposited and lacustrine beds. These unusual deposits were the result of penecontemporaneous faulting and local subsidence in the Palaeozoic basement along the line of the Sticklepath–Lustleigh fault zone.

During Neogene time the North Sea Basin continued to subside, and sediments accumulated in the Miocene and Pliocene. The Miocene and Pliocene are largely absent from onshore sites. The notable exceptions are the Coralline Crag and the Red Crag, a combined sequence of about 70 m of the Pliocene age. These are stratified cross-bedded sands containing marine invertebrate fossils which seem to have been deposited in shallow seas by tidal currents, and indicate a cooling of the climate. During Pleistocene times, as is well known, the British Isles experienced a number of cooling and warming episodes. There were as many as six cold phases during the past 2 Ma, with associated glaciation extending, at its maximum, southwards to a line roughly from London to Bristol. Pleistocene vertebrates have been found in cave deposits and in water-laid and glacial deposits. Reptiles are known, of course, exclusively from fluvial and estuarine deposits and from caves, of the warm interglacial periods.

REPTILE EVOLUTION DURING THE CAENOZOIC

After the extinction of the dinosaurs, the pterosaurs and the marine plesiosaurs and mosasaurs at the end of the Cretaceous, and the ichthyosaurs rather earlier in the Late Cretaceous, reptile evolution seemed rather less dramatic than it had been during the Mesozoic Era. The surviving reptiles included lizards, snakes, turtles and crocodilians, and terrestrial faunas were dominated increasingly by mammals. Palaeogene faunas include snakes, lizards and amphisbaenids of essentially modern type. The turtles, crocodilians and choristoderes survived the Cretaceous with little change, but the choristoderes became extinct by Oligocene times. Crocodilians continued to diversify, and several groups of terrestrial and aquatic forms radiated, but diversity plummeted towards the present day. Turtles likewise showed a number of radiations during the Tertiary in various parts of the world, but settled to a diversity pattern similar to that of today by Miocene times.

BRITISH CAENOZOIC REPTILE SITES

Fossil reptiles occur rather sporadically through most of the British Palaeogene succession (Figure 9.2). In the Late Palaeocene there are few recorded occurrences, but remains of trionychid turtles are known from the Blackheath Beds and from the Woolwich Beds. The earliest Palaeogene reptiles have recently been obtained from rare, lignite-rich clay lenses in the Reading Formation. The remains, consisting of crocodilians and turtles, occur with fish debris and are associated with a diverse flora (seeds, other plant remains and rare amber). Early Eocene reptiles are extremely well represented in the London Clay, particularly at Sheppey, where the fauna is dominated by marine forms (turtles and the aquatic snake *Palaeophis*). In the succeeding Bracklesham Group, marine reptiles again dominate. The best Late Eocene reptiles have been obtained from the Totland Bay Member of the Headon Hill Formation (Insole and Daley, 1985) of the western Hampshire coast, and from the whole of the Headon Hill Formation of the Isle of Wight. The Late Eocene faunas are dominated by terrestrial forms (lizards, trionychid turtles, crocodilians, snakes). The Oligocene Hamstead Member of the Bouldnor Formation of the Isle of Wight has produced a fauna dominated by freshwater turtles and crocodilians. The GCR scheduled sites include a selection from these Palaeogene units.

Neogene and Pleistocene reptile localities are sparse and it was hard to determine particular locations that had assessable potential for future finds; hence, none was scheduled. The Pleistocene sites are reviewed at the end of this chapter.

LATE PALAEOCENE AND EOCENE

The latest Palaeocene and Eocene series of Britain have produced significant faunas of terrestrial and marine reptiles. The remains obtained from several of the formations described above are listed by county from the Hampshire and London Basins respectively. The host formations are indicated.

ISLE OF WIGHT: Colwell Bay (Colwell Bay Member; Late Eocene; SZ 3388; 'reptiles', *Crocodilus* sp.; Insole, pers. comm. to M.J.B.); Headon Hill and Totland Bay (Totland Bay Member–Lacey's Farm Limestone Member; Late Eocene, Priabonian; SZ 3085–SZ 3287; lizards, snakes, type of *Vectophis wardi* Ford and Rage, 1980); Cliff End (middle to upper Headon Hill Formation; Late Eocene; SZ 332890; *Trionyx* sp., ?*Ocadia* sp., turtles indet., *Diplocynodon hantoniensis*, ?crocodilian, Insole, pers. comm. to M.J.B.; Gamble, 1981); Fishbourne (Fishbourne Member; Late Eocene; SZ 537941–SZ 556934; trionychid indet., *Ophisaurus, Paleryx rhombifer*, cf. *Calamagras*, erycine indet., cf. *Dunnophis*; Rage and Ford, 1980); Binstead (Seagrove Bay Member; Late Eocene; SZ 5792; 'tortoise carapaces'; Mantell, 1854, pp. 79–82, *Crocodilus* sp.); King's Quay, Wootton (Fishbourne Member; SZ 5492; lizards, turtle fragments); Ryde (upper Headon Hill Formation; Late Eocene; SZ 5992; *Trionyx incrassatus* Owen, 1849); St Helens (SZ 6289; tortoise carapaces; Mantell, 1854, pp. 79–82).

HAMPSHIRE: Warblington (Reading Formation; Late Palaeocene, Thanetian; SU 731058; crocodilian teeth; Bone, 1989, p. 151); Bishop's Waltham (Late Palaeocene; SU 5517; *Diplocynodon hantoniensis*); Southampton Docks (Earnley Member, Bracklesham Group; Mid Eocene, Lutetian, zone NP14, top zone P8 [=*coleothrypta* zone, King, 1981]; SU 4112; *Argillochelys* sp., *Trionyx bowerbanki, Palaeophis porcatus, P. typhaeus, Palaeophis* sp.); Barton Cliff (Barton Clay and Becton Sand formations; Late Eocene; SZ 305834–SZ 262922; *Trionyx planus, Argillochelys* sp., *Trionyx* sp., *'Podocnemis', 'Palaeophis'*, type of *Argillochelys athersuchi* Moody, 1980); Knight Bros., Higher Brickyard, near Bransgore (Becton Sand Formation, Horizon G; locality?; *Chelone* sp.; Burton, 1933, p. 148); Hordle Cliff (Totland Bay Member; Late Eocene; SZ 2891; lizards, snakes, amphisbaenian, types of turtles *Aulacochelys circumsulcata* Owen, 1849, *Ocadia crassa* Owen, 1849, *O. oweni* Lydekker, 1889, *Geomydia headonensis* Hooley, 1905, *Trionyx barbarae* Owen, 1849, *T. incrassatus* Owen, 1849, *T. planus* Owen, 1849, *T. rivosus* Owen, 1849, *Trachyaspis hantoniensis* Lydekker, 1889, crocodilian *Diplocynodon hantoniensis* Wood, 1844).

WEST SUSSEX: Felpham, near Bognor Regis (Woolwich and Reading beds; Late Palaeocene, Thanetian; SZ 9599; crocodilian skull, turtles; Bone, 1986); West Wittering, Bracklesham Bay (Wittering Formation, Bracklesham Group; Early Eocene; SZ 777973–SZ 793966; pelomedusid indet., *Puppigerus camperi* (Gray, 1831); *Argillochelys* sp., *Erycephalochelys fowleri* Moody and Walker, 1970 [in W9–W15 of Curry *et al.*, 1978]; 'chelonian'; Curry *et al.*, 1978, pp. 243–54; Moody and Walker, 1970; Walker and Moody, 1985); Bracklesham Bay (Earnley Formation, Bracklesham Group, beds E1–E8 of Curry *et al.*, 1978; Early–Mid Eocene), SZ 807961–SZ 823951; *Puppigerus camperi* (Gray, 1831), *Trionyx bowerbanki* Lydekker, 1889, trionychid indet.; Hooker and Ward, 1980, p. 5); Bracklesham Bay (Selsey Formation, Bracklesham Group, S1–S11 of Curry *et al.*, 1978, p. 249; Mid Eocene; SZ 825947–SZ 843932; *Argillochelys* sp., ?*Psephophorus* sp., trionychid indet.; Hooker and Ward, 1980); Bracklesham Bay (Bracklesham Group; Early–Mid Eocene; SZ 825947–SZ 843932; *Trionyx* sp., *Palaeophis toliapicus* Owen, 1841, type of *P. typhaeus* Owen, 1850, *Argillochelys* sp., type of *Gavialis dixoni* Owen, 1850, *Lytoloma* ?*trigoniceps* Owen, 1849, *Psephophorus*? sp., type of *Thalassochelys eocaenica* Lydekker, 1889, type of *Trionyx bowerbanki* Lydekker, 1889, *Crocodilus* sp., *Chelone* sp., *Pseudotrionyx* sp., chelonian indet., *Palaeophis porcatus*); Barton-on-Sea (Barton I–K; Becton Sand Formation; Mid/Late Eocene; SZ 251925–SZ 263923; Hooker and Ward, 1980, p. 6, Burton, 1929; turtle indet., *Puppigerus* sp.); Lymington (Barton Beds; Mid/Late Eocene; SZ 3493; *Crocodilus* sp., ?*Diplocynodon*, chelonian); Brockenhurst (SU 3002; *Crocodilus* sp., *Ocadia crassa*, *Trionyx* sp.).

DORSET: Highcliffe (Barton Clay Formation; Mid/Late Eocene; SZ 2192; *Argillochelys* sp., *Puppigerus* sp., trionychid indet.; Burton, 1929, 1933); Creechbarrow (Creechbarrow Limestone Formation, Mid Eocene; SY 921824; crocodilian indet., chelonian indet., cf. *Cadurceryx* sp. indet., ?lizard indet.; Hooker, 1986).

THAMES VALLEY AND ESTUARY: Abbey Wood, Kent (Blackheath Beds; Early Eocene; early Ypresian, Zone MP8–9; TQ 480786; *Trionyx silvestris*, *Trionyx* sp.; Moody and Walker, 1970; Walker and Moody, 1974; Hooker 1991); Dulwich (Woolwich Shell Beds; Late Palaeocene; Thanetian; ?TQ 3374; *Trionyx*; White, 1931, p. 9; Hooker and Ward, 1980); Herne Bay, Kent (Oldhaven Member, London Clay Formation, Early Eocene; TR 198688, TR 203688; *Chelone*, *Trionyx*; Ward, 1979; Hooker and Ward, 1980); Bellfields, Guildford (London Clay; Early Eocene; ?SU 9951; *Crocodilus*); Highgate (London Clay; Early Eocene; TQ 2887; turtle); Isle of Sheppey, Warden Point (London Clay; Early Eocene; TQ 955738–TR 024717; types of ?*Palaeaspis bowerbanki* Owen, 1842, *Argillochelys antiqua* Koenig, 1825, *Eosphargis gigas* Owen, 1861, *Chrysemys bicarinata* Bell, 1849, *C. testudiniformis* Owen, 1849, *Dacochelys delabechei* Bell, 1849, *Palaeophis toliapicus* Owen, 1841, *Crocodilus spenceri* Buckland, 1837); Old Haven, Forstall, Kent (London Clay; Early Eocene; TR 0661; *Palaeophis*); Harwich (London Clay; Early Eocene; TM 263317; *Lytoloma, Erquelinnesia, Neurochelys*; Moody, 1980b); Walton-on-the-Naze, Essex (London Clay; Early Eocene; TM 267243; *Eosphargis*, ?*Lytoloma*).

Four GCR sites have been selected from this list as those with the best potential for future finds of Palaeogene reptiles. The first, at Warden Point (Ypresian), is of historical and scientific importance for its wealth of predominantly marine reptiles. The other sites are Bartonian and Priabonian in age, and include two localities in the Barton–Hordle coast section and a third at Headon Hill on the Isle of Wight, all important for their large faunas of terrestrial and marine forms.

1. Warden Point, Kent (TQ 955738–TR 024717). Early Eocene (Ypresian), London Clay Formation.
2. Barton Cliff, Hampshire (SZ 305854–SZ 262922). Late Mid Eocene (Bartonian), Barton Clay and Becton Sand formations.
3. Hordle Cliff, Hampshire (SZ 2891). Late Eocene (Priabonian), Totland Bay Member, Headon Hill Formation.
4. Headon Hill and Totland Bay, Isle of Wight (SZ 3085–SZ 3287), Late Eocene (Priabonian), Totland Bay Member–Lacey's Farm Limestone Member, Headon Hill Formation.

WARDEN POINT, KENT (TQ 955738–TR 024717)

Highlights

Warden Point represents the richest collecting site for London Clay reptiles. Over the years, hundreds of superb specimens have been found, representing 13 species of turtles, one snake and one crocodilian. Most of these 15 reptiles were first found in the London Clay of Sheppey, and the fauna is internationally important as a key shallow marine Early Eocene fauna (Figure 9.3).

Introduction

The London Clay Formation (Figure 9.2) exposed on the northern and north-eastern shores of the Isle of Sheppey has yielded an important fauna of Eocene fossil reptiles. These include crocodilians, snakes and turtles in particular, with type specimens of eight or more species. The fossil turtles from Sheppey have been known for a long time: Parkinson (1811) noted 'two or three fossil tortoises' from Sheppey and figured a plastron and a skull, while Cuvier (1824, pp. 165, 234-5) described further remains of turtles as well as some crocodilian bones. Specimens are still being found, and the coast of Sheppey has excellent potential for future finds.

The marine London Clay Formation is up to 153 m thick (Davis, 1936), but only the top 52 m are exposed on the Isle of Sheppey. The London Clay Formation (London Clay and Claygate Beds) in the London Basin has been divided into five zones (termed A–E) on the basis of marine molluscs, and a correlation scheme based on lithology, micro- and macrofaunas, has been developed by King (1970, 1981, 1984). The Claygate Beds consist of sparsely fossiliferous alternations of marine sands and clays and are probable lateral equivalents of the highest London Clay sequences at Highgate and Sheppey. Zones A–B of the London Clay are known only from borehole records. Divisions C (12.3 m), D (16.2 m) and E (24.8 m) comprise silty clays with silt and sand partings at some levels, and beds of sandy silt. The geology of the Warden Point section (Figure 9.3) has been described by Davis (1936, 1937) and King (1970, 1981, 1984), and the reptiles by Parkinson (1811), Cuvier (1824), Owen (1841d, 1841e, 1842b, 1850), Owen and Bell (1849), Seeley (1871), Lydekker (1889b, 1889d, 1889g), Mook (1955), Moody (1968, 1974) and Zangerl (1971).

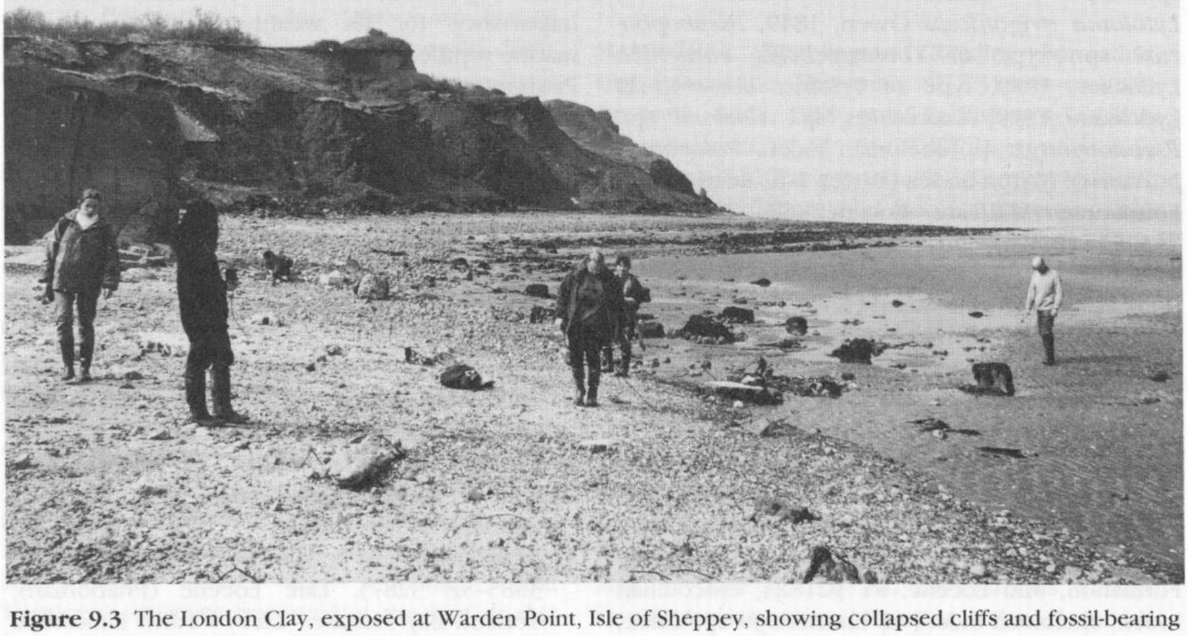

Figure 9.3 The London Clay, exposed at Warden Point, Isle of Sheppey, showing collapsed cliffs and fossil-bearing material on the foreshore. (Photo: D.J. Ward.)

Description

The main fossiliferous horizon is identified as lying in division D: 'an interval 9.5 m–16 m below the base of division E. It can be seen on the foreshore and in the base of the cliff between Eastchurch Gap and Paddy's Point (TQ 997730 to TQ 971735), and rises eastwards to a height of about 15 m O.D. at Warden Point' (King, 1981, p. 53). This bed, probably equivalent to bed C of Davis (1936, 1937) yields fishes, molluscs, brachiopods, bryozoans, crustaceans (including decapods, barnacles and ostracods), annelids, echinoderms, corals, foraminiferans and plants – a mixture of shallow-marine and drifted terrestrial forms.

Most of the published descriptions of fossil reptiles and museum specimens give no more locality information other than 'London Clay, Sheppey'. Warden Point is indicated for a turtle (BMNH R8353) and a snake (BMNH R5886), and Eastchurch for a crocodilian (BMNH R5879).

Davis (1936, p. 334) noted vertebrae of the snake *Palaeophis* 'rarely in the clay at Warden Point', scutes of *Crocodilus spenceri* at Eastchurch (TQ 997730) and vertebrae at Warden Point (TR 021725), as well as 'indeterminate remains' of turtles 'at all points of the section'. Davis (1937) further noted a specimen of the turtle *Lytoloma* from Warden Point. King (1981, p. 53) noted recent finds of vertebrae 'from nodule layers 5–10 m above the base of the exposed section', thus probably below Davis' fossiliferous horizon C mentioned above, and King (1984, p. 145) confirmed that most of the larger specimens probably came from the large phosphatic nodules in layer D. Hooker and Ward (1980, p. 5) note that fossil vertebrates on Sheppey occur at various points in the section from TQ 955738 to TR 024717. Particular fossil localities include Minster (TQ 955736), Royal Oak (TQ 967757), Bugsby's Hole (TQ 974725), Eastchurch Gap (TQ 997730), Barrow Brook (TR 013718) and Warden Point (TR 021725).

Fauna

Fossil reptile specimens from Sheppey are to be found in many British and European Museums. The best collections are in the BMNH and CAMSM. The reptile species represented are (turtles after Moody, 1980a):

	Numbers
Testudines: Pleurodira: Pelomedusidae	
?*Palaeaspis bowerbanki* (Owen, 1842)	
Type specimen: BMNH 37209	1
Testudines: Cryptodira: Cheloniidae	
Argillochelys cuneiceps (Owen, 1849)	
Type specimen: BMNH 41636	10
Argillochelys antiqua (Koenig, 1825)	
Type specimen: BMNH 49465	5
Eochelone brabantica Dollo, 1903	1
Puppigerus camperi (Gray, 1831)	4
Puppigerus crassicostatus (Owen, 1849)	5
Testudines: Cryptodira: Dermochelyidae	
Eosphargis gigas (Owen, 1861)	
Type specimen: BMNH R31	12
Testudines: Cryptodira: Trionychidae	
Trionyx sp.	4
Testudines: Cryptodira: Carettochelyidae	
Allaeochelys sp.	1
Testudines: Cryptodira: Emydidae	
Chrysemys bicarinata (Bell, 1849)	
Type specimen: BMNH 39450	2
Chrysemys testudiniformis (Owen, 1849)	
Type specimen: BMNH 39767	1
Testudines: Cryptodira: *incertae sedis*	
Dacochelys delabechei (Bell, 1849)	
Type specimen: BMNH 39257	2
Pseudotrionyx delbeidi Dollo, 1886	2
Lepidosauria: Squamata: Serpentes: Palaeophiidae	
Palaeophis toliapicus Owen, 1841	
Type specimen: BMNH 39447	14
Archosauria: Crocodylia: Neosuchia: Eusuchia: Crocodylidae	
Kentisuchus spenceri Buckland, 1837	
Type specimen: BMNH 19633	21

Interpretation

The London Clay Formation on Sheppey is interpreted by King (1984, p. 121) as a marine deposit laid down in a 'well-oxygenated low-energy shelf environment, varying in depth from *c.* 20 to *c.* 100 metres. Alternation of fine and coarser beds is ascribed to minor sea-level fluctuations. The upper part of the London Clay Formation was deposited in a progressively shallowing environment.' The bulk of the fauna, foraminifera, coelenterates, scolecodonts, serpulids, brachiopods, bryozoans, benthic molluscs, pteropods, ostracods, crustaceans, echinoderms and fishes presumably lived in the water, or in or on the sediment. Of the tetrapods, most of the turtles were indigenous marine forms, but the remainder (as with wood, leaves, pollen and spores, and insects) may have been washed in.

Following early find of turtles (Parkinson, 1811; Cuvier, 1824), further descriptions of Sheppey finds, including the erection of many new species, were given by Owen (1841d, 1842b), Owen and Bell (1849), Seeley (1871), Lydekker (1889b, 1889d, 1889g), Moody (1968, 1974) and Zangerl (1971). Owen, in his several accounts, erected 12 or more species, but many of these have been synonymized: Moody (1980a) gives an updated list of valid species. The turtles belong to several groups: Pelomedusidae, Cheloniidae, Dermochelyidae, Trionychidae, Carettochelyidae, Emydidae and *incertae sedis* (Moody, 1980a). These are mainly medium-sized marine forms, and they all have living relatives.

Palaeaspis is rather poorly known from carapace remains (Młynarski, 1976, pp. 114–15). It is a pleurodire (folds its neck sideways), belonging to the Family Pelomedusidae, which is known from the Cretaceous to the present. Modern forms occur in Africa and South America.

The other Warden Point turtles are cryptodires, forms that fold their necks vertically. *Eochelone* and *Puppigerus* (Figure 9.4A–D), both cheloniid sea turtles, are well known from a fair number of specimens from Sheppey and Belgium (body length 0.6–0.8 m) (Moody, 1974). *Argillochelys*, another cheloniid, is represented by skull and carapace remains which suggest a body length of 200 mm. The Cheloniidae have a record extending back to the Cretaceous, and they live worldwide today. *Eosphargis* (body length 1–1.5 m) is represented by skull and limb remains; it is the oldest undisputed dermochelyid turtle in the world (Benton, 1993). *Eosphargis* is known from Eocene deposits in Denmark, Belgium, and possibly offshore South Africa. The dermochelyids are now cosmopolitan. Carapace fragments of *Trionyx* sp. represent the Trionychidae, soft-shelled turtles, a widespread group of freshwater turtles known from the Cretaceous to the present. *Allaeochelys*, a carettochelyid, is represented by carapace elements. The Carettochelyidae is another marine turtle group that is present today in seas off Asia and North America, and known since the Cretaceous. The two species of *Chrysemys* (Figure 9.4E) are based on carapace remains; they are the oldest representatives in the world of Emydidae (Benton, 1993).

Pseudotrionyx and *Dacochelys* are noted as *incertae sedis* by Moody (1980a). Młynarksi (1976, pp. 73–4) had suggested that the former might belong to the carettochelyid genus *Allaeochelys*.

The snake *Palaeophis toliapicus* was described by Owen (1841e) on the basis of a partial backbone consisting of 28 vertebrae, as well as some other vertebrae and ribs (Figure 9.4I). The total length of *Palaeophis* is unknown, although Owen noted that its vertebrae were 'as large as those of a Boa Constrictor ten feet in length'. There has been some confusion over whether *Palaeophis* was a snake or a lizard, since complete skeletons are not known. Holman (1979) argues strongly that it was a snake. Further material of this genus is known from Belgium, France and Denmark (Rage, 1984), and the genus has been reported from Late Cretaceous to Late Eocene rocks of Europe, Africa and North America.

Kentisuchus spenceri was based on an incomplete skull of an animal approximately 1.5 m long (Figure 9.4H,I). Earlier, a Sheppey crocodilian (that of Cuvier, 1824) had been named *Crocodilus delucii* Gray, 1831, but the description was inadequate. Owen (1842b) ascribed other material to *K. spenceri*, and later (Owen, 1850) erected the new species *C. toliapicus* for a skull from the London Clay, and *C. champsoides* for an incomplete skull and other material from Sheppey. Lydekker (1887b, 1888a) described more Sheppey material, and reduced *C. champsoides* to synonymy with *C. spenceri*, and Mook (1955) placed them in the new genus *Kentisuchus* (Steel, 1973, pp. 69–70). *K. spenceri* is represented by skull remains, limb bones, vertebrae, ribs and scutes from Sheppey. Some remains from Bognor, Sussex and from Morocco have been ascribed to this species.

Comparison with other localities

The nearest comparable units with the London Clay Formation of Sheppey outside Britain are the Sables de Erquelinnes (Hainaut, Belgium; Late Palaeocene), the Argile d'Ypres (France, Belgium; Early Eocene), and the Sables de Bruxelles (Belgium; Mid Eocene), as well as equivalent-age units in France, Morocco, Nigeria, Mali and the eastern United States. These have yielded abundant specimens of turtles, including many that are conspecific with those from Sheppey, as well as lizards, snakes and crocodilians.

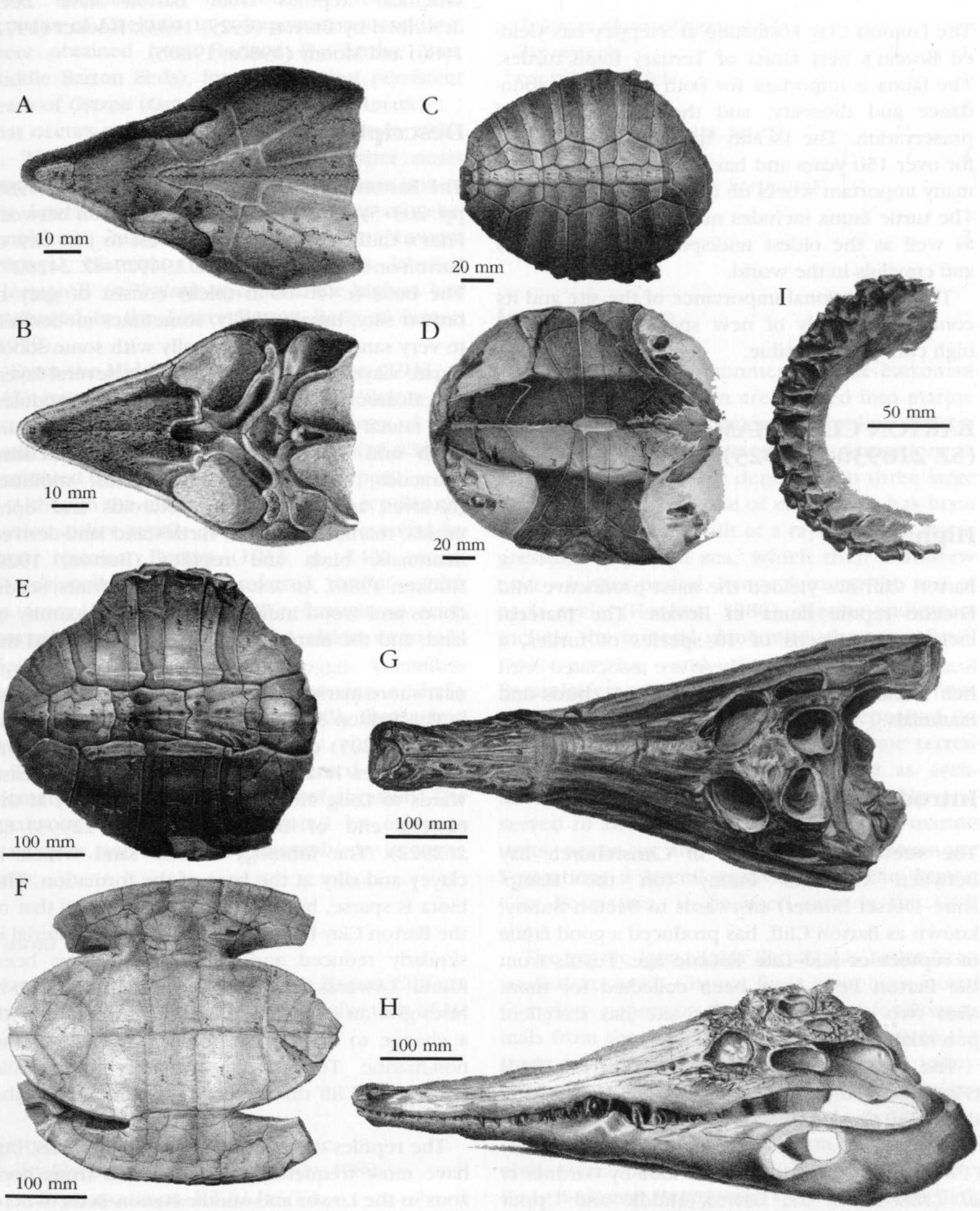

Figure 9.4 Typical reptiles of the Eocene London Clay of Sheppey. (A)–(D) The turtle *Puppigerus camperi* (Gray, 1831), skull in (A) dorsal and (B) ventral views, (C) carapace in dorsal view, (D) plastron in ventral view; (E) *Chrysemys bicarinata* (Bell, 1849), partial carapace in dorsal view; (F) *Platemys bullocki* Owen, 1841, plastron in ventral view; (G) and (H) the crocodile *Crocodilus spenceri* Buckland, 1837, skull in (G) dorsal and (H) lateral views; (I) the snake *Palaeophis toliapicus* Owen, 1841, 30 dorsal vertebrae in side view. (A)–(F) After Owen and Bell (1849); (G) and (H) after Owen (1850b); (I) after Owen (1850c).

Conclusions

The London Clay Formation at Sheppey has yielded Britain's best fauna of Tertiary fossil turtles. The fauna is important for both its relative abundance and diversity, and the good quality of preservation. The locality has been well known for over 150 years and has provided the basis for many important works on the evolution of turtles. The turtle fauna includes numerous type species, as well as the oldest undisputed dermochelyids and emydids in the world.

The international importance of the site and its continuing supply of new specimens define its high conservation value.

BARTON CLIFF, HAMPSHIRE (SZ 218930–252925)

Highlights

Barton Cliff has yielded the most productive Mid Eocene reptile fauna in Britain. The material includes specimens of 10 species of turtles, a lizard and a snake, and these are associated with rich fossils of marine shellfish, plants, birds and mammals.

Introduction

The stretch of sea cliffs in Christchurch Bay between Chewton Bunny (on the Hampshire–Dorset border) eastwards to Becton Bunny, known as Barton Cliff, has produced a good fauna of reptiles of Mid–Late Eocene age. Fossils from the Barton Beds have been collected for more than two centuries and the site has excellent potential for further finds.

The stratigraphy of the marine Barton Beds (Figure 9.2) at Barton Cliff has been discussed in detail by Gardner *et al.* (1888), Burton (1929, 1933), Hooker (1986) and Edwards and Freshney (1987). The succession was divided by Gardner *et al.* (1888) into the Lower, Middle and Upper Barton Beds on the basis of faunal changes through the sequence. Burton (1929) provided vertebrate and invertebrate faunal lists and lettered the Barton Beds A1–L based on different lithologies and faunal content. Hooker (1986) formally designated the Barton Clay Formation and erected the new unit, the Becton Sand Formation, for the Barton Sand of earlier stratigraphic schemes. Reptiles from Barton have been described by Burton (1929, 1933), Hooker (1972, 1986) and Moody (1980a, 1980b).

Description

The Barton Clay Formation (*sensu* Hooker, 1986, pp. 203–5) is exposed in the cliff section between Friar's Cliff, Mudeford in the west to just east of Barton-on-Sea in the east (SZ 194927–SZ 242927). The beds (*c.* 40–60 m thick) consist of grey to brown silty, usually shelly, sometimes moderately to very sandy, clay, occasionally with some subordinate clayey, sandy silts. There are several layers of calcareous phosphatic and sideritic nodules. The faunal list is large, including a fauna of shark teeth and teleosts, malacostracan crustaceans, ostracods, foraminifera, brachiopods, molluscs (bivalves and gastropods), asteroids and ophiuroids, marine mammals, turtles and land-derived mammals, birds and reptiles (Burton, 1929; Hooker, 1986). An associated flora of fruits, seeds, cones and wood indicates the close proximity of land, and the marine aspect of the fossils and the sediments suggest a predominantly low-energy near-shore marine environment for the formation.

The Becton Sand Formation (*c.* 25 m) (Hooker, 1986, p. 205) occurs in the cliff section to the west of Sea Road Gap, and may be traced eastwards to Long Mead End (Taddiford Gap) at the eastern end of Beacon Cliff (SZ 229931–SZ 262922). The lithology is fine sand which is clayey and silty at the base of the formation. The biota is sparse, but essentially the same as that of the Barton Clay below. Terrestrial fossil material is similarly reduced and no mammals have been found. Towards the top of the sequence, the molluscs give an indication of shallowing waters with a change to brackish conditions, leading to the non-marine Totland Bay Member of Hordle (Hordwell) Cliff that succeeds conformably to the east.

The reptiles come from a number of levels, but have most frequently been obtained from horizons in the Lower and Middle Barton Beds, where they are commonly associated with shell-rich clays and silts. Burton (1933, p. 140) notes that in Horizon B (Lower Barton Beds), a 'grey sandy and glauconitic clay, four feet thick, . . . portions of the costals and marginals of ?*Argillochelys* sp. are fairly common, but as so happens in respect of such material in the Barton Clay, it is fragmentary and renders even generic determination somewhat speculative.' 'Vertebrae of fishes and remains of Chelonia in a fragmentary condition' were obtained from Horizon E ('Earthy' Bed, Middle Barton Beds), from a 'thin but persistent seam of *Ostrea* (*Ostrea* cf. *flabellula* Lamark). . .' that occurs at the base of the unit (Burton, 1929, p. 229). Burton (1933, p. 135) further notes ?*Argillochelys* from Horizon A1, the lowest unit of his Lower Barton Beds. A specimen of 'chelonoidean' carapace in the British Museum (Natural History) (BMNH R8358) is labelled 'Horizon B' (=*Pholadomya* Bed), the highest bed attributed to the Lower Barton Beds of Burton (1929).

From the Middle Barton Beds, Burton (1933, p. 143) records (from Horizon D) that 'Below the actual Corbula Bed occasional symphyses of chelonia occur; . . . encrusted with crystals of selenite cemented together by a ferruginous deposit'.

Although the majority of the Barton reptiles are turtles, other reptile groups are represented by rarer remains. Burton (1933, p. 140) noted: 'Occasionally, vertebrae referred to *Palaeophis* sp. from Horizon A3, in a thin ferruginous seam towards the base which is very seldom exposed.' Hooker (1972, p. 181) reported a 'lacertilian' humerus (BMNH R8580) after sieving a shelly seam high in Bed H (=*Chama*-Bed), the second unit of the Upper Barton Beds.

The reptile fossils are all preserved as isolated elements and some show signs of abrasion. The turtles are generally represented by carapace fragments, and the snake *Palaeophis* by its vertebrae.

Fauna

Many of the reptile remains from Barton Cliff are curated in the BMNH, and in the collection of Mr J. Athersuch.

	Numbers
Testudines: Cryptodira: Cheloniidae	
Argillochelys athersuchi Moody, 1980	
Type specimen: KP BA/19/VA	1
Argillochelys sp.	6
Eochelone brabantica Dollo, 1903	1
Puppigerus camperi Gray, 1831	1
Testudines: Cryptodira: Podocnemidae	
Podocnemis?	1
Testudines: Cryptodira: Trionychidae	
Trionyx incrassatus Owen, 1849	1
Trionyx planus Owen, 1849	1
Trionyx sp.	1
trionychid indet.	1
'chelonian'	4
Lepidosauria: Squamata: Sauria	
'lacertilian'	4
Lepidosauria: Squamata: Serpentes: Palaeophiidae	
Palaeophis sp.	3

Interpretation

The depositional environments of the Bartonian of the Hampshire Basin are divided into marine and non-marine provinces by Hooker (1986). The Barton Clay and Becton Sands formations in Christchurch Bay were deposited in three large cycles. The erosive base of each cycle has been interpreted as the result of a rapid marine transgression of a shelf sea, which then withdrew over a longer period, hence forming the rest of each cycle (Hooker, 1986). Marine indicators include the mineral glauconite, the trace fossil *Ophiomorpha*, and the shelly faunas of Foraminifera, bivalves and gastropods. These sediments seem to have been deposited in marine waters up to 100 m deep. Some terrestrial mammal fossils occur, as well as archaeocete whales, which were presumably preserved *in situ* (Hooker, 1986). The non-marine units occur in the Creechbarrow Limestone Formation, a lateral equivalent of the Barton Clay Formation, to be seen outside the GCR site.

The reptile fauna from Barton has never been studied in detail. Chance finds have been noted in various papers on the geology and fossil mammals from the site. Moody (1980a) reviewed the turtle fauna, noting *Puppigerus* sp. and a trionychid indet. from Barton Beds A1–3, *Eochelone brabantica*, *Puppigerus camperi, Argillochelys athersuchi* (Figure 9.5), ?*Trionyx planus*, trionychid indet., and *Allaeochelys* sp. from Barton Beds B–H, and *Puppigerus* sp. from Barton Beds I–K. Moody (1980b) described *Argillochelys athersuchi*, a new species from bed C in the Barton Clay Formation from Barton Cliff. Other species of *Argillochelys* are known from the London Clay (Early Eocene) of the Thames Valley, and the Late Palaeocene/Ypresian of Belgium (Moody, 1980b).

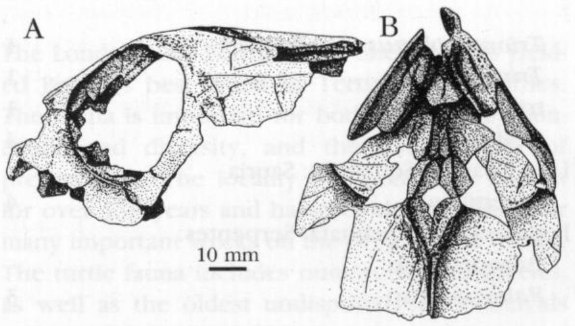

Figure 9.5 The turtle *Argillochelys athersuchi* Moody, 1980, from the Late Eocene of Barton Cliff, partial skull in (A) lateral and (B) ventral views. After Moody (1980b).

Comparison with other localities

The perissodactyl mammal *Plagiolophus curtisi* from the Middle Barton Beds is shared with the Creechbarrow Limestone Formation. The mammal fauna of the Totland Bay Member of the Headon Hill Formation, which succeeds the Becton Sand Formation, correlates with the upper part of the Calcaire de Fons at Fons; thus the Upper Barton Beds may correlate with the Robiac unit below. The Lower Barton Beds may be Marinesian, perhaps partly equivalent to the Calcaire de St Ouen, since these lie above the Bracklesham Group that are well correlated with the Auversian. The reptile fauna so far is insufficiently known to provide clear indications of relations. Its elements are known from a number of European faunas dating from Late Palaeocene to Late Eocene times.

Conclusions

Barton Cliff is the most productive British Mid Eocene site for reptiles, and source of a number of turtles, including one type specimen, as well as lizard and snake fossils. The site still yields abundant remains, and its potential has yet to be fully realized, giving it conservation value.

HORDLE CLIFF, HAMPSHIRE (SZ 253925–SZ 287915)

Highlights

Hordle Cliff has produced one of the richest assemblages of fossil reptiles and mammals from the Late Eocene in the world. The reptiles include nearly 40 species of turtles, crocodilians, lizards and snakes, and the specimens include the original named material of 15 species. New specimens come to light all the time.

Figure 9.6 The Lower Headon Beds of Hordle Cliff, looking towards Becton Bunny. (Photo: D.L. Harrison.)

Hordle Cliff

Introduction

The Late Eocene (Priabonian) Totland Bay Member of the Headon Hill Formation (formerly the Lower Headon Beds or Headon Member; Figure 9.2) exposed at Hordle Cliff (Figure 9.6), a series of low cliffs between Becton Bunny and Milford-on-Sea, have produced an important assemblage of reptiles (Figure 9.7). A recent discovery of abundant squamate remains in the Mammal Bed has greatly enlarged the faunal list, rendering the Hordle herpetofauna equal in terms of diversity to the Late Eocene herpetofaunas of continental Europe. The section is usually masked by a thin covering of talus, and some parts are heavily slipped, but the relevant horizons remain accessible and may easily be cleared. The geology of Hordle Cliff has been described by Hastings (1848, 1852, 1853), Gardner *et al.* (1888), Curry (1958), Cray (1973), Milner *et al.* (1982) and Plint (1984).

The first vertebrate remains reported from the sections of Hordle (or Hordwell) Cliff were described from the extensive collections of Searles Wood and Barbara, Marchioness of Hastings which had been assembled during the late 1840s. These remains, including numerous specimens of mammals, fishes and reptiles (crocodilians, turtles, snakes, lizards), were initially reported by Wood (1844) and Charlesworth (1845). Wood (1846) listed and figured further material from Hordle Cliff, and Hastings (1852, 1853) reported the results of six years' further collecting, listing important finds of mammals, fishes, reptiles and birds. Subsequently, in 1855, the Hastings collection was acquired by the British Museum (Natural History).

The Hordle crocodilians were discussed further by Owen (1848), Pomel (1853), Meyer (1857), Huxley (1859e) and Lydekker (1882b, 1889h). The abundant turtles from Hordle Cliff were described by Owen and Bell (1849), Seeley (1876e), Baur (1889), Lydekker (1889b) and Hooley (1905), and the snake and lizard material was described by Owen (1850), Hastings (1852), Lydekker (1888a, 1888c), Hoffstetter (1942), Sullivan (1979), Rage and Ford (1980), Estes (1983) and Rage (1984).

A recent collection of small tetrapods from Hordle Cliff made between 1976 and 1981, containing numerous new specimens, has greatly expanded the faunal list. The specimens were obtained by Mr Roy Gardner of Fareham from the Mammal Bed, from the same locality which had produced some of the Hastings material. Milner *et al.* (1982) gave reports of the new finds and identified the occurrence of 16 new taxa of lizards and snakes, some of which were previously unknown from the Eocene of the British Isles.

Description

The stratigraphy of the Early Palaeogene rocks at Hordle Cliff has been described by Gardner *et al.* (1888) and Cray (1973). The following section is abridged from Cray (1973, p. 11). All the beds dip gently south-east at about 2.5°.

		Thickness (m)
Totland Bay Member		
('Lower Headon Beds')		
	Marl	seen 0.5
	Rodent Bed: *Limnaea*	
	Marl with overlying dark clay (=Rodent Bed Marl)	0.25
	Unio Beds: grey clays with sandy layers	3.5
	Green clays	2.5
	Chara Bed: dark clays	1.4
	Blue and green clays	2.7
	Limnaea Limestone	0.4
13	Ironstone Bed	1.2
12	Crocodile Bed: sands	2.0
11	Rolled-Bone Bed: sand with abraded bones	0.3
10	Clay and sands	1.4
9(pars)	Leaf Bed: carbonaceous clay	1.0
9(pars)	Mammal Bed: clays, sands and sandy clays	3.5
8	Ironstone bed	0.4
7	Clays	1.1
6	Lignites	seen 1.4

The Totland Bay Member (Late Eocene) is included in the zone of the dinoflagellate *Wetzeliella perforata*. At Hordle Cliff the sediments form a series of low cliffs and slipped undercliffs between the east of Barton-on-Sea (just west of Becton Bunny) and Milford-on-Sea. The Mammal Bed, near the base, occurs beneath Plateau Gravel to the west of Becton Bunny, from where it may be traced as a distinct scar obliquely down the cliffs to reach sea-level just east of Long Mead End. Just east of Hordle House the highest unit in the Totland Bay Member, the *Limnaea* Marl and associated horizons, outcrops. The basal Colwell

Bay Member ('Middle Headon Beds' (pars)) are represented at Paddy's Gap by the occurrence of the Milford Marine Bed.

As has been established by Cray (1973) and Milner *et al.* (1982), among others, the Hordle reptiles were all found in the Totland Bay Member. The provenance of the early collections, however, is difficult to assess, the locality information provided by Hastings being merely 'Upper Eocene, Hordwell' or, in Lydekker's Catalogue (1888a, 1888b), 'from the Headon Beds of Hordwell'. The matrix on a number of specimens, although sparse, yields ambiguous information and cannot be used to demonstrate provenance with any degree of accuracy. Some of the specimens with adhering greenish-blue sandy clay may have come from the Mammal Bed, but other lithologies are undiagnostic. The accounts of Hastings (1848, 1852, 1853), however, indicate that most of the material came from two main horizons, the Mammal Bed and the Rodent Bed, and also from fossiliferous pockets within the Crocodile Bed.

The Rodent Bed (Hastings Bed 1), consisting predominantly of grey clays and marls, is limited in lateral extent, outcropping just to the east of Hordle House, and extending eastwards for some 275 m before wedging out. To the west the beds are absent, having been removed by recent erosion. The highest horizon of the Rodent Bed consists of clays, tinted pink and heavily altered by percolation from the overlying Plateau Gravel. These clays are underlain by a thin, dark, clayey sand which in turn rests on a comminuted shell bed, the *Limnaea* Marl.

Hastings (1852, p. 194) recorded an extensive vertebrate fauna from the Rodent Bed. The finds may be bracketed with the dark clayey marl on the basis of Hastings' detailed description of the host sediment and mention of the underlying *Limnaea* Marl. In her brief description of the fauna, Hastings (1852) recorded 'This band contains much debris, generally very compressed and fragile. You find here small rodent jaws, portions of carapace and a plastron of *Emys*, many teeth and bone fragments of crocodiles, some snake vertebrae, and rarely the teeth and bones of mammals' [translation]. Gardner *et al.* (1888, p. 596) also mention the occurrence of a large fauna from the dark clayey sand, listing 'serpents' vertebrae, rodents' teeth, etc.', but Tawney and Keeping (1883, p. 567), in their detailed stratigraphic account of Hordle Cliff, list only 'serpents' vertebrae' from the *Limnaea* Marl, without mention of the more abundant remains from the beds above.

Cray (1973, pp. 10–12) described the occurrence and preservation of the vertebrates: 'occasional rodent teeth and turtle fragments were recovered from the upper levels of the *Limnaea* marl, and the overlying dark sandy clay has yielded a moderate quantity of small-sized vertebrate debris . . . This material is always of very small size and evidently represents a current-sorted accumulation; all the large Headon Beds species are absent. All the specimens are fragmentary and . . . some of the material is water worn'.

The upper part of the Crocodile Bed is made up of fine, soft, white sands, but the lower layers are composed of more indurated sediments which are brownish in colour. The outcrop lies to the west of Hordle House, where the beds seem to rise from the base of the cliffs, and continue westwards until just west of Long Mead End. Hastings (1852, p. 198) noted crocodilians and the freshwater turtles *Trionyx* and '*Emys*' from the Crocodile Bed. *Diplocynodon hantoniensis*, collected by Wood in 1843 and described by Taylor in 1844, also appears to have come from this bed, in which the remains 'were embedded in the fine siliceous sand of which the freshwater deposit at Hordwell is chiefly composed'.

Hastings observed (1852, p. 197) that abundant shells invariably accompanied the vertebrate remains and recorded that the most richly fossiliferous level lay about 3 ft (*c.* 1 m) from the top of the bed, and that the middle of the outcrop, a little to the west of Hordle House was the most productive locality. Most material from the Crocodile Bed, however, appears to have been derived from isolated lenses rich in vertebrate remains, and such an origin is explicit in the earliest account by Hastings (1848, p. 63): 'the vertebrae and other bones of the Crocodile and *Paloplotherium* were found at intervals of from four inches to three feet apart to the westward of the heads . . . I must not omit likewise to state, that close to this crocodile's head (the whole group comprising a space of about six feet long by ten inches only in thickness, and following each other nearly in a straight line) were found the nearly entire shell of a fossil *Trionyx* . . . and the jaw, vertebrae, and scales of a fish of the order *Lepidosteus*'.

The Mammal Bed (*sensu* Curry, 1958; Cray, 1973), bed no. 9 of Tawney and Keeping (1883), and the upper part of bed 15 of Hastings, outcrops from beach level just west of Hordle House, westwards to Becton Bunny. Reptile material, although rare, was reported (Hastings, 1852) as coming from layers of white sand containing abundant remains of shells. Hastings (1852) provided a brief summary of the fauna listing '*Trionyx* and *Emys*, fragments of mammal jaws with teeth, fish vertebrae, occasional bones of birds, and some very small jaws, but no crocodiles' [translation]. The better-preserved remains appear to have come from the lowermost part of the Mammal Bed from bluish-green sandy clays, from which Hastings (1852, p. 201) recorded the dissociated remains of crocodilians, *Trionyx* and '*Emys*'. Seeley (1876e, p. 445) reported the remains of '*Emys*' from a horizon 'about 20 feet below the bed which yields the chief remains of *Crocodilus hastingsiae*, and about 10 feet above the brackish-water Upper Bagshot Beds, which are seen in the cliff rising westward at an angle of 3 degrees at Mead End', and therefore probably from the base of the Mammal Bed. Hastings (1852) also records remains from the next well-defined bed, of whitish brown sand with scattered bands of green clay, the upper half of which contained the same vertebrate material.

The specimens collected recently by Mr Gardner also derive from the Mammal Bed, from the stretch of Hordle Cliff sometimes referred to as Beacon Cliff, between Becton Bunny in the west and Long Mead End in the east (upper part of bed 15 of Hastings, 1852, Bed 9 of Tawney and Keeping, 1883). The material, consisting of many thousands of bones, all of small size, was found in numerous bone-bearing shelly pockets composed of pale-greenish, grey sand differing in some respects from the same level as described by Hastings (1852, p. 200).

Other horizons which have yielded reptile remains include the Rolled-Bone Bed. In 1852 (p. 199), Hastings reported finds of turtles and crocodilians from it. However, most of the specimens are generally highly abraded and cannot be identified precisely.

The Thin Shell Bed above the Lower Ironstone Band has yielded one of the largest collections of reptiles from Hordle. This bed occurs immediately above the ironstone band (numbered 8 in Tawney and Keepings' section), which is usually considered to mark the base of the Mammal Bed. Cray (1973, pp. 17–18), however, regards this unit as distinct on the basis of its mammal fauna, which is similar to that of a bed below the ironstone band. Hastings listed a wide range of taxa: 'You find here an equal quantity of snake and lizard vertebrae, some mammal teeth, rodent jaws, scales and vertebrae of fish, crocodile debris, *Trionyx* and *Emys*, and more rarely larger and better preserved bones including astragalus and carpal bones' [translation]. A similar fauna to the above was mentioned by Hastings as occurring in the thin white sandy marl below the lower Ironstone Band, bed No. 7 of Tawney and Keeping (1883).

Fauna

The Hastings Collection is curated in the BMNH, and other material is held in CAMSM, OUM and YORMS. Repository numbers are only given for type specimens, but an estimate of the total numbers of each species preserved in these major collections is appended.

	Numbers
Testudines: Cryptodira: Cheloniidae	
Argillochelys sp	1
Chelone sp.	1
Testudines: Cryptodira: Dermatemydidae	
Trachyaspis hantoniensis Lydekker, 1889	
Type specimen: BMNH R1443	1
Testudines: Cryptodira: Carettochelyidae	
Anosteira anglica Lydekker, 1889	
Type specimen: BMNH 33198 y,x	1
Testudines: Cryptodira: Trionychidae	
Aulacochelys (Trionyx) circumsulcata (Owen, 1849)	
Type specimen: BMNH 30404	2
Geoemyda (Nicoria) headonensis (Hooley, 1905)	
Type specimen: BMNH R1542	2
Geoemyda sp.	1
Trionyx barbarae Owen, 1849	
Type specimen BMNH 30409	2
Trionyx bowerbanki Lydekker, 1889	1
Trionyx henrici Owen, 1849	
Type specimen: BMNH 30406–7	11
Trionyx incrassatus Owen, 1849	
Type specimen: BMNH R1433	5
Trionyx planus Owen, 1849	
Type specimen: BMNH 30410,a	2
Trionyx rivosus Owen, 1849	
Type specimen BMNH 30405	1
Trionyx sp.	9+
Testudines: Cryptodira: Emydidae	
Ocadia crassa (Owen, 1849)	
Type specimen: CAMSM C20923	6+
Ocadia oweni (Lydekker, 1889)	
Type specimen: BMNH 36811	3

	Numbers
Ocadia sp.	1
Turtle indet.	100+
Archosauria: Crocodylia: Neosuchia:	
Eusuchia: Alligatoridae	
'*Crocodilus*' sp.	18
Diplocynodon hantoniensis	
(Wood, 1844)	
Type specimen: CAMSM ?unnumb.	*c.* 55
Diplocynodon sp.	*c.* 30
Lepidosauria: Squamata: Sauria	
Gekkonid	1
Necrosaurus sp.	5+
Ophisaurus sp.	50+
Anguine	5+
Glyptosaurinae *incertae sedis*	3
Plesiolacerta lydekkeri	
Hoffstetter, 1942	
Type specimen: BMNH 32840a	2
Lacertid	5+
Cordylid	50+
Squamata: Amphisbaenia: Amphisbaenidae	
Blanus sp.?	5+
Lepidosauria: Squamata: Serpentes	
Eoanilius cf. *E. europae*	1
Paleryx rhombifer Owen, 1850	
Type specimen: BMNH 25259	8
Paleryx sp.	3
Cadurcoboa sp.	1
Palaeophis	1
Calamagras sp.	50+
Platyspondylia sp.	1
cf. *Dunnophis*	5+
Vectophis wardi Rage and Ford, 1980	5+

Interpretation

Plint (1984) has interpreted the Hordle succession as representing a coastal environment, including littoral marine, barrier island shoreface, storm washover, and barrier flat, brackish lagoon, distributary channel and floodplain lake environments. The sequence indicates reducing salinity through time, and a transition towards river-dominated sedimentation in shallow floodplain lakes. Hooker (1992, p. 500) interprets the Hordle Mammal Bed as an open-forest subtropical setting. Wood (1844) and Charlesworth (1845) reported the first turtle finds from Hordle. The most abundant specimens are trionychids (soft-shelled turtles), such as the six species of *Trionyx* (Figure 9.7A) established by Owen and Bell (1849). These were based on carapace remains, such as complete scutes and fragments bearing characteristic pustulose ornament, which are of limited use in modern taxonomic schemes which rely heavily on cranial characters. Meylan (1987) provides a cladistic classification of extant Trionychidae, but makes little reference to fossil taxa. Lydekker (1889h, pp. 53–4) established the genus *Aulacochelys* on the basis of carapace remains, and assigned *Trionyx circumsulcatus* Owen (1849) to it. However, Baur (1889) argued against this, pointing out that a free border on the costals, used by Lydekker to distinguish *A. circumsulcatus*, in fact occurs widely in the Trionychidae, and hence, that the genus must be regarded as invalid. Another trionychid was named *Geoemyda headonensis* by Hooley (1905), but was regarded as a *nomen vanum* by Młynarski (1976, p. 82), and was not mentioned by Moody (1980a).

Other turtles from Hordle belong to largely marine groups, typical of most British Tertiary sites (see Sheppey report). *Argillochelys* was a moderate-sized cheloniid with an estimated total length of 200 mm. *Trachyaspis hantoniensis*, a dermatemydid, is based on limited carapace remains showing a distinctive ornament (Lydekker, 1889h, p. 54). *Anosteira anglica*, established by Lydekker (1889h, p. 54) on the basis of carapace remains, is a carettochelyid. Młynarski (1976, p. 73) was uncertain of the systematic position of the species, while Moody (1980a) assigned it to *Allaeochelys*. *Ocadia crassa* Owen, 1849 (Figure 9.7B) and *O. oweni* Lydekker, 1889 are emydids, characterized by relatively thin unornamented scutes. The species '*Emys*', widely reported by the early authors, is probably referrable to this genus. Młynarski (1976) synonymized *O. oweni* with *O. crassa* and is not certain of their true affinities, while Moody (1980a) records both species of *Ocadia* from the Hordle Member.

The first recorded Hordle reptile was a crocodilian, apparently derived from the Crocodile Bed, and named *Alligator hantoniensis* by Wood (1844). The specimen, consisted of 'A great portion of the head . . . having nearly all the upper range of teeth (42 in number) remaining, along with the humerus, dermal scutae and other parts of the skeleton'. Pomel (1853, p. 383) correctly referred this species to the genus *Diplocynodon* on the basis of sharing with the French *D. ratelii* an expansion of the third lower tooth, which was nearly as much enlarged as the fourth. Meyer

(1857, p. 538) argued that *D. hastingsiae* and *D. ratelii* might be conspecific. Owen (1848) noted three more crocodilians, which he described as a gavial, an alligator and a crocodile. Huxley (1859e) described the dermal armour of *D. hastingsiae*. Woodward (1885) and Lydekker (1887b) reviewed the Hordle crocodilians, noting the synonymy between *A. hantoniensis* and *C. hastingsiae*. The material listed as *Diplocynodon* sp. and *Crocodilus* sp. also belongs to this taxon (A. R. Milner, pers. comm., 1994). *Diplocynodon hantoniensis* (Figure 9.7C, D) is a large alligator characterized by extensive development of ventral dermal armour, in addition to the distinctive features of the dentition.

The lizards from Hordle are now known from many hundreds of specimens, and eight or more genera are currently recognized as valid. The new collections include representatives of five lizard groups including a gekkonid, three anguids, two lacertids, a cordylid and an amphisbaenian (Milner *et al.*, 1982). The family Gekkonidae is represented by a single small dentary showing characteristic closure of the meckelian canal by an anterior downgrowth of the dentary. The Necrosauridae is represented by jaws and vertebrae assignable to *Necrosaurus*. Anguids are abundant in the assemblage, the commonest material belonging to a medium-sized, limbless anguine attributable to *Ophisaurus*. A smaller anguine, similar in size to the living *Anguis* (the slow worm), also occurs, but is distinguished from *Anguis* by the complete absence of neural spines on the vertebrae. Lacertids are abundantly

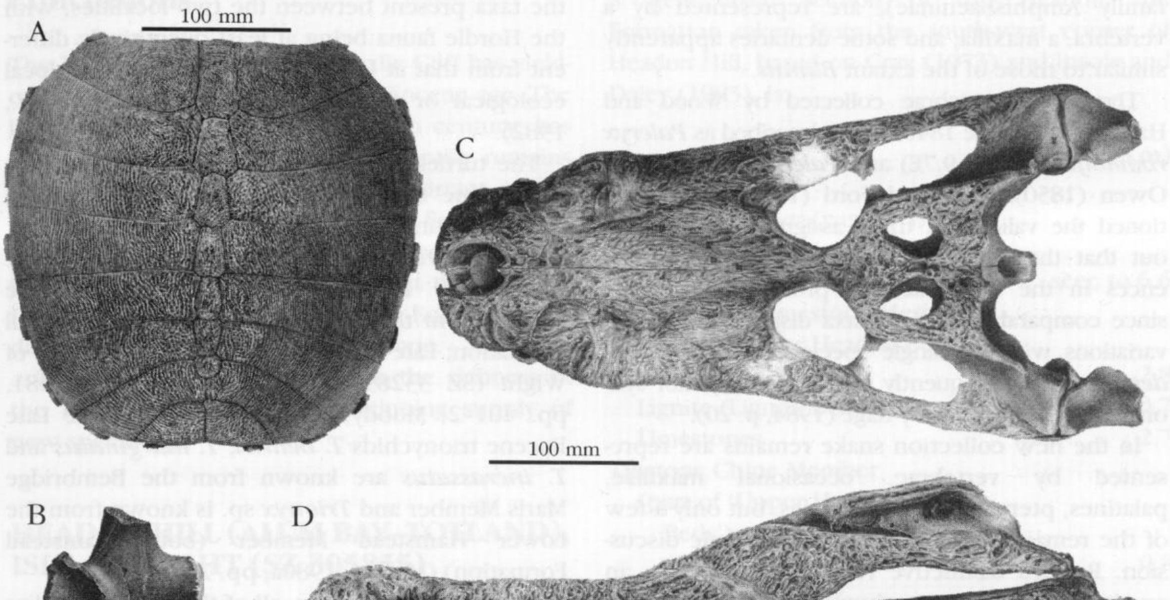

Figure 9.7 Typical reptiles of the Late Eocene Lower Headon Beds of Hordle Cliff. (A) The turtle *Trionyx henrici* Owen, 1849, carapace in dorsal view; (B) the turtle *Ocadia crassa* (Owen, 1849), internal views of plastron elements; (C) and (D) the crocodilian *Diplocynodon hantoniensis* (Wood, 1844), skull in (C) dorsal and (D) lateral views; (E) the snake *Paleryx rhombifer* Owen, 1850, mid-body vertebra in posterior, anterior, lateral, and dorsal views. (A) and (B) After Owen and Bell (1849); (C) and (D) after Owen (1850b); (E) after Owen (1850c).

represented by jaws and vertebrae, together with a few cranial and appendicular bones, and were the first lizards recognized from Hordle. The remains were originally referred to the supposed iguanid '*Iguana europeana*' by Lydekker (1888a, 1888c), but were reidentified as lacertid by Hoffstetter (1942), who designated one of the Hordle specimens the holotype of *Plesiolacerta lydekkeri* (Estes, 1983, p. 103). The other material, including vertebrae, was identified by Lydekker (1888a, 1888c) as belonging to the large limbed anguid *Placosaurus*. Sullivan (1979), however, argued that *P. rugosus*, the type species of *Placosaurus*, is indeterminate, but Estes (1983, p. 158) accepts the validity of the genus. Milner *et al.* (1982) refer *Placosaurus* to the anguid subfamily Glyptosaurinae *incertae sedis*. A large cordylid is represented by jaws and vertebrae. The burrowing lizards, the Amphisbaenidae (subfamily Amphisbaeninae), are represented by a vertebra, a maxilla, and some dentaries apparently similar to those of the extant *Blanus*.

The snake vertebrae collected by Wood and Hastings in the late 1840s were described as *Paleryx rhombifer* (Figure 9.7E) and *Paleryx depressus* by Owen (1850). Rage and Ford (1980) have questioned the validity of these assignments, pointing out that these species, designated on size differences in the vertebrae, are probably synonyms, since comparable modern taxa display similar size variations within a single species. The species *P. depressus* is consequently regarded as a junior synonym of *P. rhombifer* by Rage (1984, p. 20).

In the new collection snake remains are represented by vertebrae, occasional maxillae, palatines, pterygoids and dentaries, but only a few of the remains are suitable for taxonomic discussion. Besides distinctive remains of *Paleryx*, an erycine is the most abundant form present, known from caudal and trunk vertebrae with a complex morphology that most closely resemble those of *Calamagras*. Vertebrae bearing a distinct haemal keel are referred by Milner *et al.* (1982) to cf. *Dunnophis*. However, a haemal keel is unknown in other *Dunnophis* material. Two probable primitive caenophidians are present. The first, bearing tall neural spines on the trunk vertebrae, is referred to *Vectophis wardi*. The second form has a broad neural arch and a reduced neural spine. This may represent a new taxon, since no other comparable material is known. An aniliid is represented by an isolated dorsal vertebra. Several boids can be distinguished from the structure of their middle and posterior trunk vertebrae, and the aquatic snake '*Palaeophis*' is represented by somewhat limited remains of vertebrae, although this is a late record of this genus which should be checked (J.-C. Rage, pers. comm., 1993).

Comparison with other localities

The Totland Bay Member of Hordle Cliff is directly correlated with the top of the same unit (Insole and Daley, 1985) at Headon Hill, Isle of Wight, on the basis of their Late Eocene (Priabonian) mammal fauna and occurrence of calcareous nannoplankton zones NP17 (Barton Clay below) and NP19/20 (Curry *et al.*, 1978). The Hordle fauna includes a range of turtles, snakes, lizards and crocodilians, comparable to the Headon Hill reptiles (see Headon Hill report), however, differences are noted in the range and abundance of the taxa present between the two localities, with the Hordle fauna being at least quantitively different from that at Headon Hill. This may be a local ecological or taphonomic effect (Milner *et al.*, 1982).

The turtles are known from several other Late Palaeocene to Early Oligocene faunas in Britain and in continental Europe (Moody, 1974, 1980a). The fresh-water *Trionyx* and ?*Ocadia* and the crocodilian *Diplocynodon hantoniensis* are known from the Cliff End Member (Headon Hill Formation; Late Eocene) at Cliff End on the Isle of Wight (SZ 332893-SZ 335895) (Gamble, 1981, pp. 401-2; Moody, 1980a, pp. 23-4). The Late Eocene trionychids *T. henrici, T. marginatus* and *T. incrassatus* are known from the Bembridge Marls Member and *Trionyx* sp. is known from the Lower Hamstead Member (both Hamstead Formation) (Moody, 1980a, pp. 23-4).

Among the squamates, all of the Hordle families are found in the Eocene of France and Germany, and only the lizard families Agamidae and Helodermatidae and the snake family Typhlopidae, present in these successions, are not represented. The lizard *Placosaurus* is recorded from the Late Eocene Phosphorites du Quercy, France and Shara Murun Formation, Mongolia, as well as the Mid Eocene of the Geiseltal, Germany, and other Palaeocene to Oligocene sites in Europe and China (Estes, 1983, pp. 158-63). *Plesiolacerta* is known also from the Late Palaeocene of Dormaal, Belgium, the Late Eocene Phosphorites du Quercy, France and possibly from the Late Palaeocene of Germany (Estes, 1983, pp. 103-4). The snake *Paleryx* is known also from the Mid Eocene of the Geiseltal, Germany (Rage, 1984, p. 20), and the other less well-defined taxa are known from Palaeocene to Oligocene units in continental Europe.

The crocodilian *Diplocynodon* was named from the Aquitanian (Early Miocene) of Allier and other sites in France. Other supposed records of *D. hantoniensis* include a partial specimen from the Mid Eocene of the Geiseltal in Germany and a partial jaw from the Early Oligocene of Borken, Lower Hessen (Steel, 1973, p. 82). Other species of *Diplocynodon* have been reported from the Mid Eocene of France, Messel and the Geiseltal, Germany, Spain and Wyoming, USA, the Oligocene of France, the Miocene of Austria and the Mid Pliocene of Bulgaria, among others (Steel, 1973, pp. 81–4).

Conclusions

The Totland Bay Member at Hordle Cliff has yielded a rich fauna of reptiles of Late Eocene age. The locality, known since the early 19th century, has continued to produce abundant reptile remains and has recently produced an important collection of squamates. These recent finds, which include a variety of forms newly recorded from the British Palaeogene, indicate that the herpetofauna of this region during the Late Eocene was as diverse as those of continental Europe.

The conservation value lies in the richness of the reptile fauna and the continuing supply of new specimens.

HEADON HILL (ALUM BAY–TOTLAND), ISLE OF WIGHT (SZ 305855)

Highlights

Headon Hill has produced a good fauna of Late Eocene reptiles, and it is especially important for the specimens of lizards and snakes. These include several specimens of the glass lizard *Ophisaurus*, the first record in Britain, as well as three species of snakes.

Introduction

The Late Eocene (Priabonian) Headon Hill Formation in their type area in the degraded coastal sections of Headon Hill, Isle of Wight (Figure 9.8), have produced in the recent past a good fauna of turtles, crocodilians, snakes and lizards (Figure 9.9). Large parts of the section are obscured by mud flows, but the relevant beds may easily be cleared for further excavation.

The Headon Hill Formation between Alum Bay and Totland has been described by Prestwich (1846), White (1921), Stinton (1971), Cray (1973), Daley and Edwards (1974), Daley and Insole (1984) and Insole and Daley (1985). Accounts of the reptilian faunas have been given by Cray (1973), Meszoely and Ford (1976) and Rage and Ford (1980), but there is as yet no complete overview.

Description

A generalized section of the Headon Hill Formation taken from the south-west corner of Headon Hill, based on Cray (1973) and Insole and Daley (1985), is:

	Thickness (m)
Cliff End Member (part of 'Upper Headon Beds')	
Clays and marls	seen to 6.6
Hatherwood Limestone Member (part of 'Upper Headon Beds')	
Limestones	2.8
Lignite (Lignite Bed)	0.7
Limestones	2.7
Linstone Chine Member (part of 'Upper Headon Beds'); white and grey sands (*Microchoerus* Bed at base)	0.8
Colwell Bay Member ('Middle Headon Beds')	
Blue-green clays and sands	2.0
Limnaea Limestone	0.2
Blue, green and brown sandy clays (*Venus* Bed)	*c.* 4.4
Sands, clays and lignites (*Neritina* Bed)	2.5
Totland Bay Member ('Lower Headon Beds')	
Limnaea limestone (How Ledge Limestone)	*c.* 2.0
Marls, clays, sands and lignites	4.6
Limnaea limestone	0.4
Green clays and pale sands	4.4
Limnaea limestone	0.8
Blue and green clays	1.0

Figure 9.8 Alum Cliff, at the southern end of the Headon Beds outcrop on Headon Hill, Isle of Wight. (Photo: M.J. Benton.)

	Thickness (m)
Limnaea limestone	0.25
Green sandy clays	0.7
Green clays	seen 1.1

Cray (1973, p. 24) mentions fragments of turtle bones and, more rarely, broken mammalian remains from a limestone immediately below the Lignite Bed, a horizon outcropping about a third of the way up the vertical cliff formed by the limestone on the south-west seaward face of Headon Hill. The limestone (which may also overlie the Lignite Bed in places) is very variable lithologically, and several subdivisions were recognized. The reptile-bearing lithology is a soft, impure, orange-coloured, marly limestone, rich in the shells of *Galba* sp. However, reptile debris, including dermal scutes of turtles ('*Emys*' sp.) and teeth of the crocodilian *Diplocynodon*, also occurs sporadically throughout the Lignite Bed and appears to come from all the lithologies, being represented both in friable lignite and in the shell marls (Cray, 1973, p. 25).

In the early 1970s large collections of reptiles (particularly squamates) and amphibians were obtained by Mr R.L.E. Ford from units in the Totland Bay Member, in particular from Bed HH2 (Bosma, 1974, fig. 9) beneath a unit of hard limestone named the 'How Ledge Limestone', from a series of green-grey clays. Two localities have yielded herpetofaunas from this stratum: in the undercliff at Headon Hill and in Totland Bay. The How Ledge Limestone occurs along the coast between Hatherwood Point and How Ledge, and it appears that the reptiles occur patchily beneath the entire length of the outcrop. The fossils are all represented by disarticulated, and frequently abraded and fragmented, elements, which indicate considerable predepositional disturbance.

Fauna

The main collections of fossil reptiles from Headon Hill are curated in the BMNH as well as the Museum National d'Histoire Naturelle (MNHN) Paris and the Stuttgarter Museum für Paläontologie (Ford collection). The collections include many mammal and amphibian taxa, as well as reptiles. Amphibians include palaeobatrachid and discoglossid frogs (Figure 9.9A).

Testudines: Cryptodira: Emydidae
'*Emys*' sp.
Archosauria: Crocodylia: Neosuchia: Eusuchia
Diplocynodon sp.
Crocodilus sp.
Lepidosauria: Squamata: Sauria
Scincomorph indet.
Necrosaurus sp.
Ophisaurus sp.
Glyptosaurine indet.
Lepidosauria: Squamata: Serpentes
Paleryx rhombifer Owen, 1850
Vectophis wardi Rage and Ford, 1980
Type specimen: MNHN CGB 27
cf. *Dunnophis*

Interpretation

The Headon Hill Formation falls in the Headonian European mammal age and is equated with the upper part of this age, dated as late Late Eocene (Priabonian) by Curry *et al.* (1978). The environments are interpreted as floodplain and lagoonal, as for Hordle (q.v.), and the vertebrates are associated with closed, subtropical forests (Hooker, 1992). The squamates from the HH2 bed are associated with abundant amphibian remains, including three anurans (Discoglossidae indet., Palaeobatrachinae indet. and cf. *Eopelobates*) and rare salamanders such as 'cf. *Megalotriton*' (Rage and Ford, 1980).

The turtle '*Emys*' is represented by numerous thin unornamented scutes and appendicular bones. This genus may almost certainly be attributed to the well-known Eocene genus *Ocadia*, of which two forms have been noted from the Totland Bay Member by Moody (1980a, p. 24). A large number of isolated teeth have been collected from various parts of the section at Headon Hill; these are referred to the crocodilians *Diplocynodon* and *Crocodilus*.

The lizards from Headon Hill include members of the Necrosauridae (*Necrosaurus*), Scincomorpha and Anguidae (glyptosaurine, *Ophisaurus*), all of which are known from the Hordle Cliff section (see above). The faunal list from the HH2 horizon at Headon Hill is smaller than that from the Totland Bay Member at Hordle, lacking the gekkonid, cordylid and the lacertid *Plesiolacerta lydekkeri*.

The Scincomorpha are represented by several remains of dentary bones, but these are not entirely diagnostic. The dentaries possess a narrow meckelian groove that is shallow and restricted to the lower surface of the dentary anteriorly. The cylindrical teeth show pleurodont implantation, and (viewed laterally) are high relative to the average height of the dentary.

Ophisaurus (the glass lizard) is the most abundant lizard present, being represented by numerous distinctive remains of osteoscutes (or

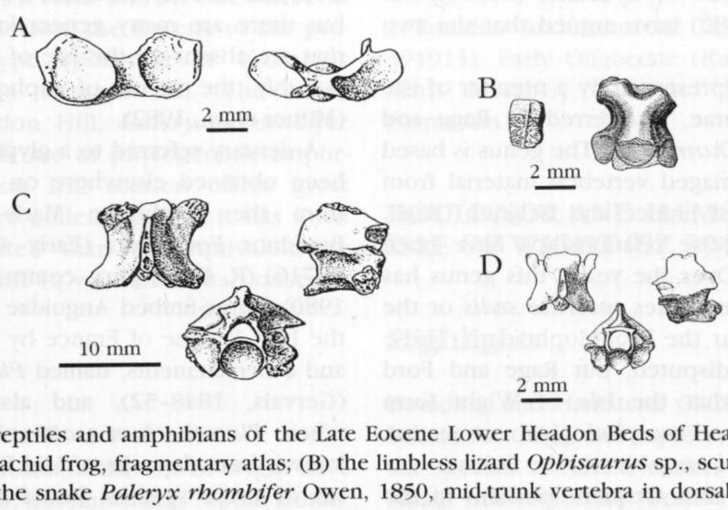

Figure 9.9 Typical reptiles and amphibians of the Late Eocene Lower Headon Beds of Headon Hill and Totland Bay. (A) A palaeobatrachid frog, fragmentary atlas; (B) the limbless lizard *Ophisaurus* sp., scute and trunk vertebra in ventral view; (C) the snake *Paleryx rhombifer* Owen, 1850, mid-trunk vertebra in dorsal, lateral, and anterior views; (D) the snake *Vectophis wardi* Rage and Ford, 1980, mid-trunk vertebra in dorsal, lateral and anterior views. (A), (C) and (D) After Rage and Ford (1980); (B) after Meszoely and Ford (1976).

osteoderms) and a few isolated dorsal vertebra (Meszoely and Ford, 1976; Rage and Ford, 1980; Figure 9.9B). The osteoscutes are flattened structures from the trunk and tail, bearing a smooth anterior 'gliding' surface and a flattened face with an ornament of irregularly branching grooves and ridges. Many of the osteoscutes, particularly those of the tail, carry a prominent median ridge. The osteoscutes and vertebrae of *Ophisaurus* show little morphological variation, and it has been hard to divide the genus into species (Rage and Ford, 1980). Meszoely and Ford (1976) suggested that the Headon Beds form was conspecific with *Ophisaurus ballensis* (Kuhn, 1940) from the Geiseltal deposits (Mid Eocene) near Halle, Germany, based on its European occurrence and Late Eocene age. This view was tentatively accepted by Rage and Ford (1980).

The anguine subfamily Glyptosaurinae is represented by two partly fragmented dorsal vertebrae and a caudal vertebra. These are larger than those of *Ophisaurus* and may be distinguished by the slightly concave ventral surface of the centra (a feature characteristic of limbed Anguidae). The necrosaurid *Necrosaurus* is represented by a single elongate posterior caudal vertebra, showing no fused haemapophyses, but two articular facets for the chevron and a groove on the ventral surface.

Of the snakes, the boid *Paleryx rhombifer* (Figure 9.9C), tropidophid cf. *Dunnophis* and caenophid *Vectophis wardi* are all represented by isolated remains of vertebrae. *Paleryx rhombifer* (represented by approximately 20 vertebrae) was regarded as congeneric with *Paleopython* from the Eocene of France by Lydekker (1888c), but Rage and Ford (1980) have argued that the two forms are distinct.

A small snake, represented by a number of isolated dorsal vertebrae, is referred by Rage and Ford (1980) to cf. *Dunnophis*. The genus is based on limited and damaged vertebral material from the Early Eocene of France and Belgium (Rage, 1984), and its precise relationships have been hard to establish. Over the years, this genus has been assigned to Serpentes *incertae sedis* or the Boidae (in particular the Tropidopheidae). These views have been disputed, but Rage and Ford (1980) suggested that the Isle of Wight form might provide a good morphological connection between 'typical' *Dunnophis* and the Boidae.

Vectophis wardi is a frequent element in the fauna, being represented by five vertebrae from Totland Bay and by about 60 vertebrae on Headon Hill (Figure 9.9D). This is a small alethinophidian snake with a distinctive vertebral morphology. The type specimen (MNHN CGB 27), collected from Totland Bay, consists of a single mid-trunk vertebra which carries a tall neural spine, a feature shared by several specimens from Hordle Cliff, which have consequently been referred to the species (Milner *et al.*, 1982, p. 152). Other features of the genus include a vaulted neural arch, robust neural spine, narrow centrum, mid and posterior trunk vertebrae which lack a hypophysis, a distinct and rather sharp haemal keel, grooves lying on either side of the haemal keel, absence of long prezygapophysial processes, and caudal vertebrae with pleurapophyses and haemapophyses. On the basis of these characters, Rage and Ford (1980) consider *Vectophis* as perhaps belonging to the Colubroidea, and as possibly a primitive member of this superfamily.

Comparison with other localities

Geographically and stratigraphically, the nearest comparable units to the Totland Bay Member at Headon Hill are the same stratigraphic unit at Hordle Cliff (SZ 253925–SZ 287915; see above), and the Fishbourne Member ('Osborne Beds') at Fishbourne (SZ 551927). In the 'Osborne Beds' shared faunal elements include *Ophisaurus* sp., *Paleryx rhombifer* (represented by one rounded and worn trunk vertebra) and cf. *Dunnophis*. The Erycinae cf. *Calamagras* and Erycinae unidentif. (Rage and Ford, 1980), present in these beds, do not occur in the Totland Bay Member. All of the reptiles recorded from Headon Hill are known from the directly correlative sequence at Hordle, but there are many genera known from Hordle that are absent on the Isle of Wight (see above), possibly the result of taphonomic differences (Milner *et al.*, 1982).

A dentary referred to a glyptosaurine lizard has been obtained elsewhere on the Isle of Wight, from the Bembridge Marls Member of the Bouldnor Formation (Early Oligocene) (BMNH R8716) (R. Estes, pers. comm. to Rage and Ford, 1980). Large-limbed Anguidae are represented in the Late Eocene of France by cranial osteoderms and other elements, named *Placosaurus rugosus* (Gervais, 1848–52), and also from Germany, where *Placotherium waltheri* (Weigelt, 1929) is known from deposits of Mid Eocene age. The status of these species, based mainly on external morphology of the osteoderms, is not clear and, although clearly belonging to the Glyptosaurinae, both forms are regarded by Sullivan (1979, pp. 43–4) as *nomina dubia*. In North America glyptosaurine lizards are represented by more complete remains bearing similar osteoderms, and numerous genera have been named, particularly from the Eocene and Oligocene (Sullivan, 1979; Estes, 1983).

The discovery of the anguid *Ophisaurus* from the Isle of Wight, extends the range of this genus from the Mid and Late Eocene of central Europe, to the British Isles. The genus is still extant and is confined to the eastern section of continental Europe.

Necrosaurus is known from the Late Eocene of France (*Necrosaurus cayluxi* Filhol, 1873) and from the Mid Eocene of Germany and latest Eocene and Early Oligocene of France (*N. eucarinatus* Kuhn, 1940). The genus is also known from the Paleocene of France and from the Early Oligocene of Belgium (Estes, 1983).

The snake *Dunnophis* is reported from the Early Eocene of France and Belgium, the Mid and Late Eocene of North America, the Late Eocene of France and the Early Oligocene of Belgium (Rage, 1984). As noted above, the closely related Totland Bay Member form cf. *Dunnophis*, may be phylogenetically intermediate between *Dunnophis* and the Tropidophiidae; in this sense, it is confined to the British Early Eocene.

Conclusions

Headon Hill is an important reptile site of Late Eocene age, unique for its record of the glass lizard *Ophisaurus*, a form known elsewhere in continental Europe from the Eocene to the present day. The type specimen of *Vectophis wardi* came from Headon Hill. The other snakes from Headon Hill, *Paleryx rhombifer* and cf. *Dunnophis* are of phylogenetic importance. The Headon Hill section offers great potential for future collecting, and it has been much less exploited than the equivalent-age units at Hordle Cliff (q.v.), hence its conservation value.

OLIGOCENE

The Oligocene deposits of the Isle of Wight have produced restricted, but important, reptile faunas. The finds are dominated by remains of freshwater turtles and crocodilians, but other elements include fully terrestrial forms including snakes. The better-documented localities include the following:

ISLE OF WIGHT: Thorness Bay (Bembridge Marls Member; Early Oligocene, Rupelian; SZ 455935; *Trionyx incrassatus*, *Trionyx* indet.; Hooker and Ward, 1980, p. 9; Daley, 1973, pp. 83–93); Gurnard Bay (=Gurnet Bay; Bembridge Marls Member, marine band; Early Oligocene, Rupelian; SZ 4795; *Trionyx incrassatus*, *T. circumsulcata*, '*Emys*' sp., trionychid indet., snake, *Diplocynodon hantoniensis*; Daley, 1973, Hooker and Ward, 1980, p. 9); Whitecliff Bay (Bembridge Marls Member; Early Oligocene, Rupelian; SZ 643864; turtle, *Trionyx*); Bembridge (Bembridge Marls Member; Early Oligocene, Rupelian; SZ 6588; *Trionyx* sp., *T. incrassatus* Owen, 1849, trionychid indet.; Hooker and Ward, 1980, p. 9); Bouldnor and Hamstead Cliffs (Bembridge Marls Member, Hamstead Member; Early Oligocene, Rupelian; SZ 391913; crocodilians, *Ocadia crassa*, *Trionyx* sp., *Diplocynodon hantoniensis*, *Diplocynodon* sp., *Paleryx* sp.); Yarmouth (Bembridge Marls Member; Early Oligocene, Rupelian; SZ 367899; trionychid indet.; Hooker and Ward, 1980, p. 8); Hamstead (=Hempstead; Hamstead Member, mottled clays and marls?; Early Oligocene, Rupelian; SZ 4091; *Trionyx* sp, 'chelonian', *Paleryx depressus, Crocodilus hastingsii, Diplocynodon hantoniensis*; Hooker and Ward, 1980, p. 9).

One GCR site has been selected for British Oligocene reptiles:

1. Bouldnor and Hamstead Cliffs, Isle of Wight (SZ 391913). Early Oligocene (Rupelian), Bembridge Marls Member, Hamstead Member, Bouldnor Formation.

BOULDNOR AND HAMSTEAD CLIFFS, ISLE OF WIGHT (SZ 391913)

Highlights

Bouldnor and Hamstead Cliffs is the only site in Britain for Oligocene reptiles, the fauna of five or six species of turtles, snakes and crocodilians is small, but important worldwide because of the general rarity of Oligocene reptiles sites everywhere.

Introduction

The Bembridge Limestone Formation and Bouldnor Formation (Figure 9.2) exposed at Bouldnor Cliff have produced the best fauna of British Oligocene reptiles. Large areas of the cliff are affected by landslips and debris flows, but exposures on the foreshore, visible at low water, are normally excellent and many new finds could be made.

The cliff sections at Hamstead and Bouldnor cliffs have been described by Forbes (1856), White (1921), Daley (1972, 1973), Daley and Edwards (1974) and Insole and Daley (1985).

Reptile remains have been noted sporadically by authors on the stratigraphy of the site, but there are no comprehensive descriptions. Hooker and Ward (1980) summarize the fauna, while Moody (1980a) gives some details of the turtles.

Description

At Bouldnor Cliff the whole of the Bouldnor Formation (Cranmore Member, Hamstead Member, Bembridge Marls Member; *c.* 87 m) and underlying Bembridge Limestone Formation are exposed. The Bembridge Limestone Formation, with the Late Eocene/Osborne Member below, occurs in the east of the section in Hamstead Ledge (SZ 401920), where three freshwater limestone beds are developed. West of Hamstead Point sections are seen in the top of the Bembridge Limestone Formation, the whole of the overlying Bembridge Marls Member and part of the Hamstead Member.

The Bembridge Marls Member here comprises 21.5 m of fresh- and brackish-water sediments, mainly clays and silts, and contain an abundant, but taxonomically restricted, molluscan fauna (Daley, 1972). The lower part of the unit occurs in the cliffs, but the sequence is best exposed on the foreshore and may be seen at low tide immediately to the west of Hamstead Ledge where numerous shell beds are developed in green or grey muds. All of the beds become visible at low water during the equinoctial spring tide. The Bembridge Oyster Bed (Forbes, 1856) (Bed HAM I of the Bembridge Marls Member), also seen at Whitecliff Bay, occurs at the base of the succession. The restricted assemblages include taxa which are regarded by modern analogy as brackish-water forms. The rest of the sequence is made up of grey to bluish-grey silts and clays deposited variously under fresh- and brackish-water conditions. Beds HAM XXIII–XXV (Daley, 1973) contain abundant monocotyledonous leaf fragments and the water-plant seeds *Brasenia* and *Stratiotes*, which occur in bands with the gastropods *Viviparus* and *Galba* (a pulmonate).

The Black Band, taken to mark the base of the Hamstead Member, occurs low in the cliffs about 200 m east of a line of posts. This comprises a carbonaceous mud and contains freshwater gastropods such as *Viviparus*. At the base of the unit, autochthonous root systems penetrate into the underlying bed. Another black, lignitic clay (the *Nematura* Bed) occurs somewhat higher up in the Hamstead Member succession, but contains a distinctive brackish-water molluscan fauna. The greater part of the Hamstead Member consists of grey-green and green muds with occasional dark-brown to black, laminated muds. However, these are much obscured by recent mudflows.

The succeeding Cranmore Member (9.2 m) is marked by a sudden change from brown-grey to bright green clay. The member occurs in the top of the cliff at the west of the exposure where it is capped by 'Plateau gravel'. The member is divided into the *Corbula* Beds (marine) and the *Cerithium* Beds (non-marine), which together consist of a mixture of grey, blue and black fossiliferous clays.

The section is based on White (1921, pp. 133–4, 140–1), Daley (1973), Daley and Edwards (1974), Daley and Insole (1984) and Insole and Daley (1985).

	Thickness (m)
Solent Group	
Bouldnor Formation	
Cranmore Member (Upper Hamstead Beds of White, 1921)	
Corbula Beds	5.8
Cerithium Beds	3.4
Hamstead Member (Lower Hamstead Beds of White, 1921)	
Green and mottled clays, with lignite beds and shell beds	*c.* 25
Water-Lily Bed: laminated lignite with seeds, palm leaves, water lily leaves and molluscs	0.6
Green and red marls (much obscured)	*c.* 2
White Band: green clays with white shell-marls	1.8

	Thickness (m)
Green clay with ironstone nodule band (much obscured)	10.8
Nematura Bed: black lignitic clay, full of gastropods	0.9
Green and black clays, with bivalves and gastropods	8.1
Black Band: lignite, full of *Paludina* and *Unio*	0.5
Bembridge Marls Member (Bed notation from Daley, 1973)	
HAM XXXI–XXXIV: green, red and mottled clays	10.2
HAM XXX: lignite with seeds and molluscs	0.6
HAM XXVI–XXIX: clays with seeds and molluscs	*c.* 5.0
HAM XXIII–XXV: lignite and clay, rich in water-plant seeds, leaf fragments, and gastropods	*c.* 2.0
HAM XX–XXII: freshwater clays and silts	1.6
HAM XIX: green clays and white marls, with bivalves	0.2
HAM XVI–XVIII: green mudstone and lignite band	15
HAM XV: black clay with gastropods	0.9
HAM XI–XIV: mudstones and siltstones, with bivalve band	3.3
HAM VI–X: grey and blue-green laminated clays, with brackish-water bivalves and gastropods	2.7
HAM V: greenish-grey clay with bands containing *M. acuta, Serpula* sp. and *Viviparus lentus*	0.3
HAM I–IV: grey and black clays with shelly partings and bands containing bivalves and gastropods; thin shell bed with *Ostrea* at the base	0.9
Bembridge Limestone Formation	

In the Bembridge Marls Member, vertebrate material is quite common, but usually comminuted. Fish vertebrae are mentioned by Daley (1972) as occurring commonly at many horizons, whereas fish scales and teeth are found in others. It is possible, but not proven, that the larger reptile and mammal remains may also derive from particular levels.

Fauna

Faunal lists are summarized by Hooker and Ward (1980) and Moody (1980a), but fuller accounts are not yet available. The specimen counts are based on collections in the BMNH and IWCMS.

	Numbers
Testudines: Cryptodira: Trionychidae	
Ocadia crassa (Owen, 1849)	1
Trionyx sp.	3
Lepidosauria: Squamata: Serpentes	
Paleryx sp.	1
Archosauria: Crocodylia: Neosuchia: Eusuchia: Alligatoridae	
Diplocynodon hantoniensis (Wood, 1944)	several
Diplocynodon sp.	several
crocodilian	several

Interpretation

Daley (1973) postulated three main environments of deposition for the Bembridge Marls Member. In the lower part the Bembridge Oyster Bed, which coincides with the main transgressive period of the Bembridge Marls Member, is interpreted as an estuarine deposit, since the sediments contain few primary sedimentary structures, and a fauna consisting predominantly of comminuted *Ostrea* shell debris indicates a considerable amount of water movement, in contrast to the fauna of lagoonal environments. Daley (1972) noted that the molluscan assemblages from this part of the succession are comparable with those of tropical and subtropical mudflats of the present day. The predominantly grey or blue-grey clays which form the bulk of the Bembridge Marls Member are interpreted as lagoonal in origin; the bivalves are commonly in life position, and some of the sediments exhibit varve-like lamination. On the basis of sedimentary evidence (ripples, irregular lamination, presence of lignite) the central and upper parts of the deposit are thought to represent floodplain and lacustrine deposits.

The trionychid turtles are represented by recent finds of complete carapaces and limited skull material (in IWCMS). The new trionychid carapaces fall into high- and low-domed types. The high-domed forms show great variation in the cross-sectional thickness of their shells, whereas in the low-domed forms the carapace is of uniform thickness. One of the specimens exhibits 'pathological' distortion of the rear dorsal surface of the carapace. The new skull material consists of a partial braincase with both quadrates attached. There are some associated postcranial remains of cervical vertebrae, but no carapace or lower jaw. New finds also include specimens of the crocodilian *Diplocynodon*, which had an estimated length of about 4 m.

Comparison with other localities

The Bembridge Marls Member has been correlated on the basis of mammals and charophytes with the Tongrian Stage in Belgium and the Ludian (Late Eocene) in the Paris Basin (Curry *et al.*, 1978). There has been some controversy over whether the beds should be included in the Eocene or Oligocene, but most British workers consider them as belonging to the latter.

Oligocene trionychids have been recorded from Monteviale in Italy (*Trionyx capellini*), Steiermark, Austria (*T. styriacus*), Catalonia (*T. marini*) and China (*T. gregaria*) (Młynarski, 1976, pp. 77–9). The crocodilian *Diplocynodon* has been reported especially from the Late Eocene Headon Beds of Hordle and Headon Hill (see above), as well as from sediments ranging in age from the Early Eocene to Miocene of Europe and the USA (see Headon report).

Oligocene reptiles are known from North America and Europe, but finds are much rarer than for those of Eocene or Miocene age. The famous Quercy deposits in France span the Eocene–Oligocene boundary, and thus equate in age with the Bembridge Marls. These have produced a diverse array of lizards, snakes, crocodilians and turtles. Other continental European Oligocene localities are spread as far afield as Spain and the Ukraine, and Germany and Italy. The mammals have been heavily studied, the reptiles less so. It is hard to make detailed comparisons with the Hamstead–Bouldnor locality until the reptiles from the site are more fully described.

Conclusions

Britain's only Oligocene reptile site, and one of the few of that age in the world. This international importance, plus the continuing opportunities for new finds provided by erosion, establish the site's conservation value.

PLEISTOCENE

Fossil reptiles from the British Pleistocene are presently known from interglacial sediments of Cromerian, Hoxnian, Ipswichian and Holocene age at a wide variety of localities, owing mainly to the result of a recent programme of research carried out by J.A. Holman in collaboration with A.J. Stuart and other workers during the 1980s and 1990s. The reptiles form part of herpetofaunas which are of value as reliable indicators of Pleistocene climates and environments. The finds also provide a valuable contribution to knowledge on the diversity and spread of reptiles through Pleistocene time, and demonstrate a link with climatic fluctuation. The localities are listed by county, and include only those that have produced reptiles (amphibian-only sites are not listed).

DEVON: Cow Cave, Chudleigh (SX 8679; *Anguis fragilis*); Happaway Cave, Torquay (Flandrian; *Natrix natrix*; Holman, 1987).

SOMERSET: Westbury-sub-Mendip (Cromerian; ?zone Cr IV; ; *Emys orbicularis*, *Coronella austriaca*, *Natrix natrix*, *Vipera berus*; Stuart, 1979; Holman, 1993).

SUSSEX: Selsey (Ipswichian; zones Ip Ib–IIb; *Emys orbicularis*; Stuart, 1979); Amey's Eartham Pit, Boxgrove (unnamed interglacial between Cromerian and Anglian; SU 920085; *Anguis fragilis, Lacerta* cf. *L. vivipara, Natrix natrix, Natrix* sp.; Holman, 1993).

KENT: Dierden's Pit, Ingress Vale, Swanscombe (Hoxnian; ?zone Ho III; TQ 6074; *Emys orbicularis, Natrix natrix*; Stuart, 1979; Holman, 1987); Ightham Fissure, near Ightham (Devensian–Holocene; TQ 5956; *Anguis fragilis, Natrix natrix, Vipera berus, Coronella austriaca*; Newton, 1894a; Holman, 1985).

SUFFOLK: Bobbitshole, Ipswich (Ipswichian; zones Ip Ia–IIa; *Emys orbicularis*; Stuart, 1979); Stoke Tunnel, Ipswich, Suffolk (Ipswichian; Stoke Tunnel 'Bone Bed', ?zone Ip IV; *Emys orbicularis*; Stuart, 1979); Harkstead (Ipswichian, ?zones Ip III–IV); *Emys orbicularis*; Stuart, 1979).

ESSEX: Cudmore Grove, East Mersea, Mersea Island (Hoxnian, Substage Ho IIIb, channel fill; TM 068146; *Emys orbicularis, Anguis fragilis, Lacerta* *vivipara, Lacerta* sp., *Elaphe longissima, Natrix maura* or *N. tessellata, Natrix natrix, Natrix* sp. indet., *Vipera berus*; Bridgland, 1987, p. 329; Holman *et al.*, 1990); Little Oakley (Cromerian Stage; Little Oakley Silts and Sands; TM 223294; *Emys orbicularis*; Bridgland, 1987, p. 321).

NORFOLK: Mundesley (Ipswichian; 'Forest Bed'; ?= Mundesley Sands, zones Ip Ib–IIb; TG 3136; *Emys orbicularis, Emys lutaria, Tropidonotus natrix*; Newton, 1862, 1879, 1882a; Woodward, 1880; Stuart, 1979); West Runton; Bacton (TG 1842; *Tropidonotus natrix, Vipera berus, Anguis fragilis*; Upper Freshwater Bed, Cromerian, W. Runton; *Natrix natrix, N. vipera*; Newton, 1882a, 1882b; Holman, 1993); Itteringham Gravel Pit (from Ipswichian interglacial bed; TG 139305; *Emys orbicularis, Natrix natrix*; Hallock *et al.*, 1990); East Wretham (Holocene; zone II (=VIIa, Atlantic); *'Emys lutaria', Emys orbicularis*; Newton, 1862; Woodward, 1880, Stuart; 1979); Swanton Morley (Ipswichian; zone Ip IIa; *Emys orbicularis*; Stuart, 1979).

LANCASHIRE: Dog Holes, Warton (Flandrian; SD 4128; *Anguis fragilis, ?Vipera, Natrix natrix*; Holman, 1987).

None of these sites could be selected as having a greater or lesser claim to be selected as a candidate GCR site to represent British Pleistocene reptiles. Indeed, several have been entirely worked out, and new ones are found when suitable sites are excavated.