Pollen and dinoflagellates from the Red Crag at Walton-on-the-Naze, Essex: evidence for a mild climatic phase during the early Late Pliocene of eastern England

MARTIN J. HEAD*

Department of Geology, Earth Sciences Centre, University of Toronto, Toronto, Ontario M5S 3B1, Canada

(Received 17 March 1988; accepted 11 July 1998)

Abstract – Spot sampling of the Red Crag Formation at Walton-on-the-Naze, Essex (= Walton Cray) has revealed a diverse record of dinoflagellates, pollen, and other palynomorphs. Pollen from a basal horizon is dominated by *Pinus*, but also contains high values of *Sciadopitys* and a small but diverse component of deciduous mesothermal trees. *Taxodium* is more common at 2 m above the base of the Red Crag and may represent a different part of a climate cycle. A mild- to warm-temperate climate is inferred for the Walton assemblages and a correlation with the Reuverian B pollen substage (Late Pliocene, 3.0 to > 2.6 Ma) is demonstrated, thereby constraining the timing of an important marine transgression in eastern England.

Dinoflagellates from the basal horizon and from 2 m above the base of the Red Crag generally indicate a restricted marine environment, but outer neritic to oceanic dinoflagellates are occasionally present, and imply the penetration of more saline North Atlantic water masses into the southern North Sea basin. Mild- to warm-temperate conditions are indicated by the presence of several thermophilic species. The Walton assemblages have strong similarities with those of the mid-Pliocene Coralline Crag Formation of eastern England, but differ in the presence of *Bitectatodinium tepikiense*, which, along with an apparently reduced species richness, gives evidence of cooler conditions. A number of thermophilic species at Walton are not reported from younger Pliocene deposits in eastern England, perhaps reflecting a less equable climate after Northern Hemisphere cooling at 2.55 Ma.

1. Introduction

Sea cliffs just north of Walton-on-the-Naze, Essex expose one of the most important and fossiliferous sections in UK Neogene stratigraphy (Balson, 1995). Marine, shelly, quartz-rich sands of the Upper Pliocene Red Crag Formation extend here for about 300 m along the coast, yielding an exceptionally diverse molluscan fauna that has attracted serious study for more than 130 years. The Red Crag has an extensive coverage in southern East Anglia (Mathers & Zalasiewicz, 1988), and it was soon recognized that the deposits at Walton (Fig. 1) are among the oldest on account of their molluscan fauna with its many extinct species, and taxa of Mediterranean affinities (Wood, 1866). Using evidence from molluscs Wood (1866) proposed a three-fold subdivision of the Red Crag, the lowest of which he named the Walton Crag for the deposits at Walton-on-the-Naze. This became the basis of Bell's (1887) and Harmer's (1900a, b) Waltonian (lowermost) subdivision of the Red Crag, again based mainly on molluscs. The Walton deposits have been assigned on lithostratigraphic grounds to the Walton Crag Bed of the Red Crag Member and Formation by Funnell & West (1977) where they continue to be placed at the base of the Red Crag Formation (Funnell, 1996).

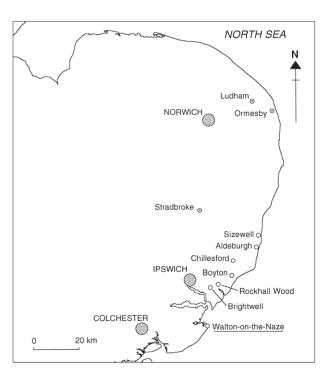


Figure 1. Map of eastern England showing the location of Walton-on-the-Naze and other sites mentioned in the text. Major cities are also shown.

The Red Crag at Walton-on-the-Naze lies directly on the London Clay (Lower Eocene), as it does in many other parts of East Anglia. In a few localities,

^{*} E-mail: head@quartz.geology.utoronto.ca

and in some areas of the southern North Sea, the Red Crag rests unconformably on the mid-Pliocene Coralline Crag, indicating a regional hiatus of perhaps nearly a million years, during which time extensive erosion took place. The precise duration of this hiatus is uncertain, but the lower part of the Coralline Crag is tentatively placed at between 3.8 and 3.6 Ma (latest Early Pliocene; Jenkins & Houghton, 1987). The Red Crag at Walton-on-the-Naze (Walton Crag) probably correlates with the Upper Pliocene molluscan Mol C Zone of the Netherlands (Meijer & Preece, 1995) which has been assigned to the upper part of the Reuverian pollen stage (Zagwijn, 1974). Planktonic microfossils are poorly represented at Walton-on-the-Naze, owing to its restricted marine character, and this has hindered direct correlation to standard marine biostratigraphies. Benthic foraminifers from a basal horizon at Walton-on-the-Naze have been correlated indirectly with the Reuverian C pollen substage (about 2.55 to slightly older than 2.60 Ma) of The Netherlands (Funnell, 1961, 1996); and a pollen assemblage recovered from these basal deposits has also been compared with the Reuverian C (Hunt, 1989; Bowden, Hunt & Green, 1995). However, this assemblage was subsequently reassigned, albeit without discussion, to the Reuverian B (Gibbard et al. 1991), which spans about 3.0 to slightly older than 2.6 Ma. Ostracode evidence constrains the age to younger than 2.9 Ma (Wood et al. 1993), this being consistent with Reuverian B or C correlations. The basal Red Crag at Walton-on-the-Naze is therefore equivocally dated, although it clearly predates the full effects of Northern Hemisphere cooling at about 2.55 Ma based on its warm-water faunal associations.

The Red Crag at Walton-on-the-Naze is about 4-5 m thick and consists largely of subtidal cross-bedded shell sands. These were deposited by migrating sand waves under strong tidal currents in up to 20-30 m of water (Dixon, 1979; Balson, 1990, 1995, 1997). Although the deposits show a high degree of lateral variability, two cross-bedded units are often seen, and these may overlie a poorly stratified basal horizon (e.g. see Kendall, 1931, fig. 1). Each cross-bedded unit represents the lateral migration of a single sand wave, and its deposition is estimated to have taken as little as 10 years (Balson, 1997 and pers. comm.). The hiatus separating the two units is unlikely to be stratigraphically significant (Balson, 1997). This implies that the entire cross-bedded part of the Walton Crag may represent an extremely short duration of geological time, although the basal horizon might be appreciably older. The deposits are now extensively oxidized, owing to their high permeability and position above the water table, and are thus generally unsuitable for palynology. However, the basal horizon has locally escaped oxidation to a thickness of about 0.5–1.5 m, probably since it occurs within the low water table that overlies the London Clay here. Hunt (1989) recovered a palynological assemblage in a single sample from these basal deposits. The present study is based on three samples from similar deposits and one sample from a ferruginous siltstone lamina 2 m above the base. It provides more detailed palynological information, and helps to refine the correlation and palaeoclimatic interpretation of this important section. This study also shows that palynomorphs are locally present within the oxidized zone, implying that more detailed stratigraphic investigations may be worthwhile in the future.

2. Materials and methods

Five samples, labelled WC1 to WC5, were collected from separate points along the Naze Cliffs within a 100 m stretch immediately north of the Naze Tower car park (TM 265234). Four samples (WC1-3 and WC5) are from the lowest 5 cm of a 0.5-1.5 m-thick horizontal layer of Walton Crag that directly overlies the London Clay. This layer is weakly consolidated, and consists of greyish to buff-coloured, coarse, poorly sorted, shelly sands. It is poorly bedded, which suggests bioturbation. Three of the samples (WC1-WC3) were calcareous and contained in situ palynomorphs, but one sample (WC5) was decalcified and essentially barren except for some reworked palynomorphs. This sample is not discussed further. Sample WC4 was from a moderately calcareous, redstained, silty lamina up to about 1 cm thick occurring 2 m above the base of the Walton Crag. It appears to be traceable laterally over tens of metres, and is not associated with the strong cross-bedding that develops higher in the sequence. This lamina yielded abundant but variably preserved palynomorphs.

Samples were dried and weighed, decalcified in $10\,\%$ cold HCl, diluted with water in a large beaker, and then stirred thoroughly to suspend the fine particles, which were decanted into another beaker. This was done repeatedly until all fines had been collected. After addition of one *Lycopodium* spore tablet (batch #710961; for one tablet X = 13,911, $s = \pm 689$, and V = 4.95%), the concentrated fine fraction was further demineralized in cold 48% HF. The organic residue was given brief ultrasound (15 seconds) and sieved at 10 um. Residues were stained with safranin-O and mounted on microscope slides with Cellosize and Elvacite. The sieved residue was mounted on 50×24 mm coverslips, one each for samples WC1 and WC3 and two each for samples WC2 and WC4. Only for sample WC4 was any residue left over.

All slides were examined at \times 25 magnification to determine species present. Only two samples (WC2 and WC4) were sufficiently well preserved for counting, and marginally so (especially WC4). Counts were made using a $100\times$ oil objective. Many of the bisaccate conifer grains were broken, and so large fragments were counted as fractions and added to the whole specimen count. Dinoflagellates were similarly counted:

indeed fragments of Bitectatodinium tepikiense and Lingulodinium machaerophorum dominated the assemblages, even though complete specimens were scarce. Some reworked dinoflagellates (mostly from the underlying London Clay) were easily discriminated on the basis of preservation and stratigraphic range, but longranging, thin-walled, indeterminate Achomosphaera and Spiniferites species were not. These were assumed reworked unless well preserved, and so may be considerably under-represented in the counts. Reworked spores and pollen were recognised mostly by preservational differences in samples WC1-WC3, but this was difficult for sample WC4 where preservation (corrosion and compression) was very variable. In practice, sporomorphs were counted as in situ unless strongly compressed or corroded. Owing to the limitations imposed by preservation, all counts must be considered as broad estimates rather than absolute values.

All data for the four samples analysed are presented in Table 1, and illustrations of palynomorphs are given in Figs. 2–4. Selected taxa are discussed in Appendices 1 and 2. This paper follows the ecological classification of Hall (1964), the time scale of Berggren *et al.* (1995), and the dinoflagellate taxonomy of Head (1994, 1996, 1997). The age and correlation of stages for the Pliocene period of eastern England are given in Head (1998a).

3. Spores and pollen

Samples from the basal horizon of the Walton Crag (WC1–WC3) appear broadly similar in species abundances and composition (Table 1), and all three are treated as a single assemblage. Sample WC4 was collected from 2 m above the base of the Walton Crag and yielded a distinctive pollen assemblage. It is discussed separately.

3.a. Assemblage from the basal horizon

The assemblage is based on three samples, although only one was countable (WC2). It is dominated by Pinus (at least 46.8% and perhaps more owing to fragmentation of specimens), with gymnosperms making up at least 71.7% (Table 1). Dominance by *Pinus* is generally considered characteristic of boreal forests; but the assemblage also contains important temperate coniferous elements, including Tsuga (3.4%) and especially Sciadopitys (9.5%; Fig. 2e, f), which is strongly associated with the Middle Miocene (subtropical) browncoal forests of central Europe and is represented today by a single upland species known to be intolerant of cool-temperate (and cooler) conditions (Schweizer, 1980, p. 305). Sequoia, a thermophilic conifer, appears to be rare. However, small and usually split inaperturate pollen, sometimes with a short ligula, reach almost 10%. They are assigned to Taxodium-type and Juniperus-type, depending whether or not a ligula was seen, and represent a significant combined cupressacean (cosmopolitan) and taxodiacean (warm) component. The angiosperms represent only 15% of the spore-pollen sum and are well represented by heathland (Ericales, 5%) and coastal saltmarsh (e.g. Chenopodiaceae–Amaranthaceae, 2.3%) species.

Of the arboreal species, a number of temperate—especially warm-temperate—taxa are present in small numbers including *Carya, Corylus*-type (Fig. 2s), *Ilex, Juglans, Myrica*-type (Fig. 2t), *Pterocarya, Quercus*-type, *Tilia,* and *Ulmus*. In addition, the form species *Nyssapollenites kruschi* (Fig. 2l–r) and *Tricolporopollenites parmularius* (Fig. 2g, h) are probably related to the extant thermophiles *Nyssa* and *Eucommia* respectively. Fern spores do not give strong clues as to the regional climate, but their relatively low species richness, together with an absence of palaeotropical species, points to conditions cooler than subtropical.

The climatic interpretation of this assemblage is necessarily cautious—marine-deposited pollen assemblages are well known to include pollen from a variety of distant sources, as well as being commonly overrepresented by bisaccate pollen such as *Pinus*. On balance, it nevertheless appears that, despite strong dominance by *Pinus*, an important mesothermal element including *Sciadopitys* contradicts exclusively boreal forest. Consequently, the regional vegetation is interpreted as temperate coniferous forest with some broad-leaved deciduous trees that together reflect mild-temperate conditions.

The spore-pollen assemblage is undoubtedly assignable to the Reuverian pollen stage of The Netherlands on the basis of numerous Tertiary-relict taxa, including Nyssapollenites kruschi, and an absence of several warm-temperate to subtropical indicators (e.g. Palmae, Symplocos, and high values of Sequoia-type) that characterize the subjacent Brunssumian pollen stage (Zagwijn, 1960; van der Hammen, Wijmstra & Zagwijn, 1971). Assignment to a substage within the Reuverian is more subjective. These substages are largely based on differing abundances of taxa, particularly Pinus (abundant in substages A and C), rather than the presence or absence of specific taxa. The Reuverian B is a warmtemperate substage characterized by deciduous and mixed mesophytic forest, whereas the Reuverian C is a transitional boreal pine forest substage followed by tundra vegetation of the Praetiglian Stage (Zagwijn, 1960). Even in The Netherlands these substages cannot always be recognized (Zagwijn, 1960), and pollen assemblages from latest Reuverian marine deposits in The Netherlands may have inconsistent characteristics (de Jong in Gibbard et al. 1991). Given the coniferdominant aspect, but with a varied deciduous forest component for the basal Walton assemblage, comparison is made with a cooler interval of the Reuverian B. This assignment is consistent with pollen records for Brittany (France), where an upsection decrease in

Table 1. Palynomorphs recorded in the present study.

Sample number	WC1	WC2	WC3	WC4
nvertebrates				
nvertebrate remains	+	11	+	+
Angiosperm pollen				
Alnus 4-pored	+	3 (0.3%)	+	+
Alnus 5-pored Artemisia sp. of Zagwijn, 1960		1 (0.1%)	+	8 (1.4%)
Betula	+	1 (0.1%)		+
Carya		1 (0.1%)		1 (0.2%)
Caryophyllaceae	+	4 (0.4%)	+	1 (0.2%)
f. Rosaceae Chenopodiaceae–Amaranthaceae	+	+ 26 (2.3 %)	+	9 (1.5%)
Compositae, Liguliflorae-group (=Lactuceae)	т	20 (2.3 %)	+	9 (1.3 %) +
Compositae, Tubuliflorae-group		2 (0.2%)	+	+
Corylus-type (Fig. 1s)	+	10 (0.9%)	+	+
Bricales (Timber 1)	+	55 (5.0%)	+	23 (4.0%)
Fraxinus (=Tricolpites hians Stanley) f. Fraxinus		4 (0.4 %) 1 (0.1 %)		
Gramineae (= Graminidites sp.)	+	9 (0.8%)	+	1 (0.2%)
lex	+	2 (0.0 7 0)		+
<i>Tuglans</i>			+	
Liquidambar				+
Lonicera xylosteum-type (=Lonicerapollis gallwitzii Krutzsch, o.c.) Myrica-type (Fig. 1t)		1 (0.1%)	+	+
Nuphar cf. lutea (=Nupharipollis echinatus Krutzsch)		1 (0.1 /0)	Т.	+
Vyssapollenites kruschi (Potonié) (Fig. 11–r)	+	17 (1.5%)	+	+
Populus		3 (0.3%)		
Pterocarya, 5-pored	+	5 (0.5%)	+	
Pterocarya, 6-pored Quercus-type	+	3 (0.3 %) 9 (0.8 %)	+ +	+ +
Salix	'	4 (0.4%)	+	+
Sparganium		. (0.1.70)		+
Taxus		6 (0.5%)		
Tilia		+		+
Fricolpopollenites sp. Fricolporopollenites parmularius (Potonié) (Fig. 1g, h)	+	1 (0.1%)		+
rricoiporopouenties parmutarius (Fotonie) (Fig. 1g, 11) Reticulataepollis pseudointergranulatus (Potonié) sensu Sontag, 1966 (reworked?) (Fig. 1i,		+		т
ricolporopollenites spp.	, 3/	+		
Tetracolporopollenites sapotoides Thomson & Pflug (reworked?) (Fig. 1k, 1)		+		
Ulmus-Zelkova, 4-pored		+		1 (0.2%)
Ulmus-Zelkova, 5-pored Fotal angiosperms	+	1 (0.1 %) 167 (15.0 %)	+	1 (0.2%) 45 (7.7%)
otal angiosperius		107 (13.0 70)		43 (7.770)
Gymnosperm pollen		0 (0 50)		
Abies ndeterminate inaperturate grains	+	8 (0.7%)	+	120 (20.7%)
funiperus-type (probably includes <i>Taxodium</i> -type where ligula is obscured)	+	98 (8.8%)	+	8 (1.4%)
Picea	+	13 (1.2%)		1 (0.2%)
Pinus sylvestris-type sensu Zagwijn, 1960 and indeterminate Pinus	+	520 (46.8%)	+	219 (37.7%)
Pinus-haploxylon sensu Zagwijn, 1960		+		1 (0.2%)
Podocarpidites libellus (Potonié)	+	1 (0.1%)	+	+ 20 (3.4%)
Sciadopitys (Fig. 1e, f) Sequoia-type	т	105 (9.5 %) 1 (0.1 %)	т	24 (4.1%)
Taxodium-type sensu Zagwijn, 1960	+	12 (1.1%)	+	41 (7.1%)
Tsuga canadensis-type		8 (0.7%)		` ′
Tsuga heterophylla-type	+	29 (2.6%)	+	4 (0.7%)
Tsuga sp. indet. Zonalapollenites igniculus (Potonié)		1 (0.1%)		
Zonalapollenites rueterbergensis Krutzsch		т		+
Total gymnosperms		796 (71.7%)		438 (75.4%)
Embryophyte spores		1 (0 10/)		
Baculatisporites quintus (Thomson & Pflug) Camerozonisporis cf. minoris Krutzsch (reworked?)		1 (0.1 %) 1 (0.1 %)		+
Cingulatisporites sp.		1 (0.1 %)		+
Laevigatosporites ĥaardti (Potonié & Venitz)	+	10 (0.9%)	+	+
Leiotriletes wolffii Krutzsch (o.c.)			+	5 (0.9%)
	+	14 (%)	-	2 (0.5 / 0)
Lycopodiella cf. inundata	++	. /	Т	` ′
Neogenisporis sp. (Fig. 1a, b)		2 (0.2%)	Т	+
Neogenisporis sp. (Fig. 1a, b) Obtusisporis sp. (Fig. 1c, d)		. /	Т	` ′
Neogenisporis sp. (Fig. 1a, b)		2 (0.2 %) 1 (0.1 %)	+	+ 1 (0.2%)

Table 1 (cont.)

Sample number	WC1	WC2	WC3	WC4
Stereisporites spp.	+	6 (0.5%)	+	1 (0.2%)
Verrucatosporites poriacus (Krutzsch) poriacus Krutzsch (reworked?)		1 (0.1%)		5 (1.200)
Total embryophyte spores		42 (3.8 %)		7 (1.2%)
Undetermined sporomorphs	+	105 (9.5%)	+	91 (15.7%)
Total in situ embryophyte spores and pollen		1110 (100%)		581 (100%)
Reworked sporomorphs	+	128	+	12
Fungal spores				
Glomus sp.		1		
Tetraploa aristata type a of Ellis, 1949		+		
Miscellaneous spores Fungal hyphae	++	24 26	+	+ +
Tungar nyphae	·	20	•	
Freshwater algae		2		
Botryococcus Debarya sp. (= Lecaniella sp.)	+	3		+
Gelasinicysta vangeelii Head			+	+
Planctonites sp.		+		
Sigmopollis carbonis (Newman)	+	1		
Sigmopollis hispidus Hedlund	+	+	+	+
Miscellaneous algae				
Leiosphaeridia sp. of Head, 1993	+	10	+	+
Micrhystridium spp. of Head, 1993	+	129	+	19
Dinoflagellates				
Undetermined Achomosphaera Spiniferites spp.*†	+	75 (30%)	+	37 (24.3 %)
Achomosphaera andalousiensis andalousiensis (autonym) (Fig. 2k)*†	+	1 (0.4%)		1 (0.7%)
Amiculosphaera umbracula Harland*† ? Ataxiodinium zevenboomii Head*	+	1 (0.4 %) 1 (0.4 %)	+	+
Barssidinium pliocenicum (Head) (Fig. 2a, b)*		1 (0.4%)	+	1 (0.7%)
Bitectatodinium raedwaldii Head (Fig. 2i, j)*	+	14 (5.6%)	+	6 (3.9%)
Bitectatodinium tepikiense Wilson (columellate luxuria) (Fig. 2g, h)†	+	15 (6%)	+	21 (13.8%)
Bitectatodinium tepikiense Wilson (vermiculate luxuria)† Gen. et sp. indet. (Fig. 3e)		1 (0.4%)	+	
Geonettia sp. of Head, 1997 (Fig. 3d)*		+		1 (0.7%)
? Impagidinium aculeatum (Wall)*	+			` /
Lejeunecysta marieae (Harland) (Fig. 2d)†		+		
Lejeunecysta sp. (Fig. 2c) Lingulodinium machaerophorum (Deflandre & Cookson) (Fig. 3a)*†	+	+ 38 (15.2%)	+	15 (9.9 %)
Nematosphaeropsis lemniscata Bujak (Fig. 3b, c)*	+	5 (2%)	'	+
Operculodinium centrocarpum sensu Wall & Dale, 1966 (Fig. 3f)†	+	36 (14.4%)	+	61 (40.1%)
Operculodinium? eirikianum Head et al. (Fig. 3h, j)*†		+		+?
Operculodinium israelianum (Rossignol) (Fig. 3g)† Round brown cysts*†	+	51 (20.4%) 3 (1.2%)	+	9 (5.9 %)
Spiniferites mirabilis (Rossignol) (Fig. 21)*†		2 (0.8%)	+	
Spiniferites ramosus (Ehrenberg)*†		6 (2.4%)	+	
Tectatodinium pellitum Wall (Fig. 2e, f)*	+	+	+	+
Total in situ dinoflagellates		250 (100%)		152 (100%)
Reworked dinoflagellates		254		79
Marine algae incertae sedis				
Nannobarbophora walldalei Head†		4		3
Cymatiosphaera? invaginata Head et al. (Fig. 3i, k) Tasmanitids	+	+ 8	+	6
Palynomorph concentrations Lycopodium spike for non-marine palynomorphs and miscellaneous algae		963		2
Lycopodium spike for dinoflagellates and marine algae incertae sedis		963		38
Dry weight of sample (in grams)	167	139	195	103
Estimated concentration of <i>in situ</i> embryophyte spores and pollen per gram dry weight		115 (± 7%)		39,234 (± 70 %)
Estimated concentration of in situ dinoflagellates per gram dry weight		26 (±9%)		540 (± 19%)

Samples WC1–WC3 are from the basal horizon of the Walton Crag, and sample WC4 is from two metres above the base. A cross (+) indicates taxa recorded outside of counts. Percentages of individual pollen and embryophyte spore taxa refer to the total *in situ* pollen and embryophyte spore count (1110 grains for WC2 and 581 grains for WC4), including unidentified grains, but excluding reworked grains. Percentages of individual dinoflagellate taxa refer to the total *in situ* dinoflagellate count (250 grains for WC2 and 152 grains for WC4), excluding reworked cysts. An asterisk (*) against dinoflagellate names denotes taxa also present in the mid-Pliocene Coralline Crag (Head, 1997, 1998a, b), and a dagger (†) marks those taxa known from younger deposits in eastern England or the southern North Sea (Head, 1994, 1996, 1998a). O.c. = orthographic correction in accordance with ICBN Art. 60.11.

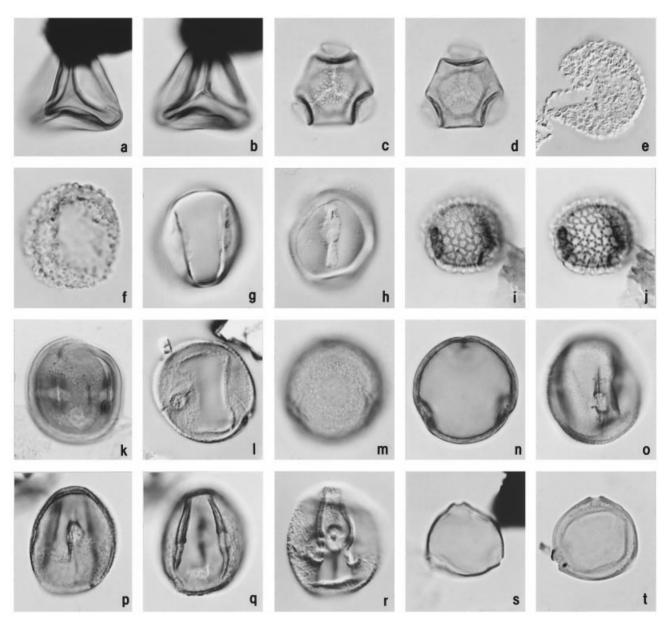


Figure 2. Selected spores and pollen from the basal Walton Crag at Walton-on-the-Naze. (e, g, h, l, r) are interference contrast images, the others are in bright field. Max. dia. = maximum diameter. Various magnifications. (a, b) *Neogenisporis*? sp. Upper and lower focus. Sample WC2(1); T19/0. Max. dia. = $26 \, \mu m$. (c, d) *Obtusisporis* sp. Lower and upper focus. Sample WC2(1); T33/4. Max. dia. = $23 \, \mu m$. (e, f) *Sciadopitys*. (e) Sample WC2(2); F53/1. Max. dia. = $40 \, \mu m$. (f) Sample WC2(1); U14/2. Max. dia. = $27 \, \mu m$. (g, h) *Tricolporopollenites parmularius* (Potonié). Mid and upper focus showing tricolporoidate germinals. Sample WC2(2); R18/0. Length = $27 \, \mu m$. (i, j) *Reticulataepollis pseudointergranulatus* (Potonié) *sensu* Sontag, 1966 (reworked?). Upper and slightly lower focus showing columellae and supratectal reticulum. Sample WC2(1); E31/0. Length = $21 \, \mu m$. (k) *Tetracolporopollenites sapotoides* Thomson & Pflug (reworked?). Sample WC2(1); W20/3. Length = $26 \, \mu m$. (l–r) *Nyssapollenites kruschi* (Potonié). (l) Sample WC2(1); P15/3. Max. dia. = $31 \, \mu m$. (m, n) Upper and mid focus. Sample WC2(2); R29/4. Max. dia. = $27 \, \mu m$. (o) Sample WC2(1); W48/2. Length = $29 \, \mu m$. (p, q) Upper and mid focus. Sample WC2(1); J28/1. Length = $29 \, \mu m$. (r) Sample WC2(1); F16/0. Length = $32 \, \mu m$. (s) *Corylus*-type. Sample WC2(1); H28/3. Max. dia. = $23 \, \mu m$. (t) *Myrica*-type. Sample WC2(2); A49/4. Max. dia. = $24 \, \mu m$.

Sciadopitys gives way to an increase in *Pinus*, which in turn is followed by an increase in Gramineae (Morzadec-Kerfourn, 1977). These three events are staggered, the *Pinus* and Gramineae increases presumably signalling the beginnings of the Reuverian C and Praetiglian, respectively.

3.b. Assemblage from 2 m above the base of Walton Crag

A single assemblage from a red-stained calcareous siltstone lamina (sample WC4) contains a rich concentration of palynomorphs dominated by spores and pollen. Unfortunately, variable preservation has rendered the assemblage only marginally countable, with undetermined sporomorphs comprising more than 15% (Table 1). Even specimens within the same taxon show variability in preservation (compression and corrosion), suggesting a wide range of source environments and transport histories, and the possibility that considerable undetected reworking is recorded in Table 1. A detailed interpretation of sample WC4 is therefore not warranted, although some generalizations can be Taxodium-type and Sequoia-type pollen together comprise at least 11%, and perhaps considerably more (indeterminate inaperturate grains make up 20.7%) of the sporomorph total. Most of these grains are reasonably uncompressed, although corroded, and appear to be contemporaneous or penecontemporaneous. They represent important contributions from lowland swamp (Taxodium-type) and upland forest (Sequoia-type; along with Pinus at 37.7% and Sciadopitys at 3.4%). Heathland (Ericales, 4%) and saltmarsh (Chenopodiaceae-Amaranthaceae, 1.5%) communities are also represented. The moderate abundance of mesothermal taxa (Taxodium-type, Sequoia-type, and Sciadopitys) and the presence of Tertiary relicts (e.g. Tricolporopollenites parmularius, Nyssapollenites kruschi, and Liquidambar) together suggest a mild- to warm-temperate climate and permit assignment to the Reuverian B substage of The Netherlands.

4. Dinoflagellates and other marine palynomorphs

All three basal Walton Crag samples (WC1–WC3) appear similar in their marine palynomorph component, and are treated as a single assemblage. Sample WC4 from 2 m above the base of the Walton Crag, although generally similar, differs in the relative abundance of some taxa and is treated separately.

4.a. Assemblage from the basal horizon

The assemblage contains 22 dinoflagellate taxa (Table 1), and is dominated by the extant taxa Achomosphaera / Spiniferites spp. (at least 33.6%), Operculodinium israelianum (20.4%; Fig. Lingulodinium machaerophorum (15.2%; Fig. 4a), Operculodinium centrocarpum sensu Wall & Dale, 1966 (14.4%; Fig. 4f), Bitectatodinium tepikiense (6.4%; Fig. 3g, h), and the extinct species Bitectatodinium raedwaldii (5.6%; Fig. 3i, j). Of these, L. machaerophorum and B. tepikiense have modern regional distributions that are strongly limited by temperature. L. machaerophorum has a mild temperate to tropical North Atlantic distribution today (Harland, 1983 text-fig. 4; Dale, 1996) with highest abundances mostly below 50°N (warm-temperate to tropical), although some abundant records are in the mild-temperate zone: notably the Irish Sea (Reid, 1972), some Scottish lochs (Lewis, 1988), and the Norwegian fiords (Madsen & Dale, 1992). L. machaerophorum is presently rare on the east coast of England (Reid, 1972). Bitectatodinium tepikiense is a colder water species, with a temperate to subpolar modern distribution in the North Atlantic (Dale, 1996; but see also remarks in Appendix 1). Highest concentrations (above 10%) are in mild- to cool-temperate areas just north and east of the British Isles (Harland, 1983), although B. tepikiense is consistently present in low numbers around the coast of England and Wales (Reid, 1974). The strong representation of both L. machaerophorum and B. tepikiense therefore suggests mild- to warm-temperate waters during deposition of the basal Walton Crag, with temperatures somewhat higher than today. This is supported by the rare occurrence of Tectatodinium pellitum (Fig. 3e, f), which presently has a south temperate to tropical distribution in the North Atlantic (Harland, 1983). Warm temperatures are further implied by presence of the extinct cold-sensitive taxa: Ataxiodinium zevenboomii (questionably identified), Barssidinium pliocenicum (Fig. 3a, b), Bitectatodinium raedwaldii, Geonettia sp. of Head, 1997 (Fig. 4d), Operculodinium? eirikianum (Fig. 4h, j) and the acritarch Nannobarbophora walldalei (Head, 1993, 1996, 1997). Several of these (A. zevenboomii, B. raedwaldii, and N. walldalei) had Pliocene distributions that extended as far as the tropical-subtropical Bahamas (Head and Westphal, in press). The cold-tolerant species Habibacysta tectata Head et al. and Filisphaera filifera Bujak are notably absent from the Walton assemblage, although they occur in the younger Pliocene crag deposits of eastern England (Head, 1994, 1996, 1998a).

assemblage reflects restricted marine conditions. Neritic taxa dominate, whereas the outer neritic to oceanic taxa Amiculosphaera umbracula, Impagidinium aculeatum? (represented by a single specimen), and Nematosphaeropsis lemniscata (Fig. 4b, c) are rare. Of particular interest, L. machaerophorum is an important euryhaline species often associated today with estuarine environments (e.g. Morzadec-Kerfourn, 1977) and moderately elevated nutrient levels (Dale, 1996). **Operculodinium** israelianum presently has an estuarine to inner neritic distribution (Wall et al. 1977), and is a common constituent of shallow subtidal and intertidal deposits in later Pliocene deposits in eastern England (Head, 1998a). This species has a variable morphology in Pliocene deposits of eastern England, where it may intergrade with Operculodinium centrocarpum sensu stricto (Head, 1996). Operculodinium israelianum dominates the cold Thurnian stage of the Ludham borehole (Head, 1996; Fig. 1), indicating that this species had a relatively broad climatic range during the Pliocene, compared with its narrower, tropical to warm-temperate distribution today (Wall et al. 1977; Head, 1998a).

810 m. j. head

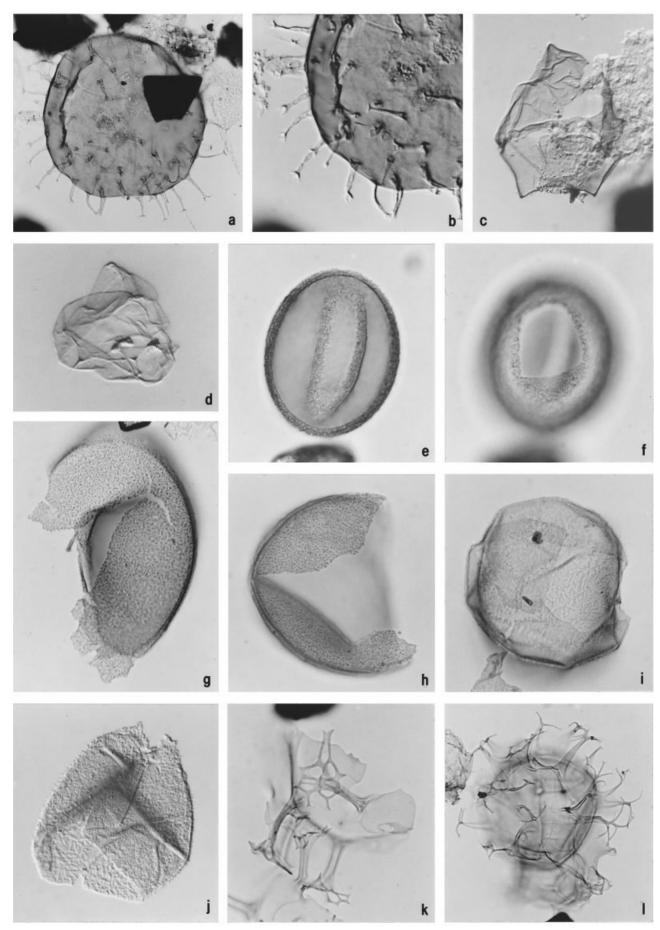


Figure 3. For legend see facing page.

4.b. Assemblage from 2 m above the base of Walton Crag

Dinoflagellates from Sample WC4 are partially oxidized, and there is no surviving evidence of protoperidinoid species except for some bleached fragments of *B. pliocenicum*. Otherwise, the assemblage is comparable with that recovered from Sample WC2, but it contains a higher proportion of *Operculodinium centrocarpum sensu* Wall & Dale, 1966 (40.1% vs. 14.4%) and reduced *Operculodinium israelianum* (5.9% vs. 20.4%). This might suggest a slightly reduced inner neritic/estuarine influence for Sample WC4, but there is no concomitant increase in oceanic species. Environmental and climatic inferences for the two assemblages do not differ appreciably.

4.c. Age significance of the dinoflagellates

Several species recorded at Walton apparently do not occur in younger deposits of the North Sea basin, and likewise a number of taxa from the Coralline Crag do not occur at Walton (see Table 1), although the ranges of these taxa are not well known. *Impagidinium multiplexum* has not been reported at Walton, although it occurs in the Pre-Ludhamian (West & Norton, 1974; Harland *et al.* 1991) and younger stages of eastern England (Head, 1998a). This species first appears at about 2.8 Ma in the western North Atlantic (De Verteuil, 1996; DSDP Hole 603C, M. J. Head, unpublished data) and the Walton assemblages conceivably pre-date this event, although this inference is obviously tentative.

5. Discussion and conclusions

Pollen from the basal horizon of the Walton Crag show similarities with Hunt's assemblage (Hunt, 1989; and listed in Bowden, Hunt & Green, 1995), also obtained from the base of the Walton Crag, but additional species are reported in the present study: *Carya* (0.1%), *Corylus*-type (0.9%), *Ilex* (<0.1%), *Juglans* (<0.1%), *Myrica*-type (0.1%), *Nyssapollenites kruschi* (1.5%), *Tilia* (<0.1%), *Tricolporopollenites parmula-rius* (<0.1%), *Sequoia*-type (<0.1%), *Sciadopitys* (9.5%), and *Tsuga* spp. (3.4%). The Taxodiaceae are possibly more abundant in Hunt's assemblage

(although this might reflect better preservation of his material) and he reported much higher values of Gramineae (11.9% vs. 0.8% for the present study). More extensive investigations of the basal Walton Crag are required to understand these differences.

Funnell (1961, 1996) compared benthic foraminifers of the basal Walton Crag with those of Zeeuwsch-Vlaanderen from which Reuverian C pollen had been obtained (Zagwijn, 1960), contrary to the Reuverian B determination of the present study. However, the pollen spectra of this Dutch site are not closely comparable with the Walton assemblage of the present study, which has more mesothermal deciduous tree taxa and higher values of *Sciadopitys*.

The pollen assemblage from 2 m above the base of the Walton Crag is broadly similar to that of the basal horizon, but has significantly higher values of inaperturate pollen including Taxodiaceae, suggesting a stronger contribution from coastal swamps, but continuance of mild- or warm-temperate conditions. Perhaps this sample represents a different part of an obliquity-forced climate cycle, given the distinctiveness of its pollen when compared with that of the basal horizon. Notably, the basal horizon has a distinctive molluscan assemblage not found higher in the Walton Crag (Bell, 1911, 1912, his "basement bed"), implying that conditions had indeed changed following deposition of the basal horizon.

In comparison with other Pliocene crag localities in eastern England, the Walton pollen assemblages are most similar to the Sudbourne Member of the Coralline Crag Formation at Rockhall Wood, Suffolk (Gibbard & Peglar, 1988; Fig. 1). This was tentatively assigned to the Reuverian C by Gibbard and Peglar, but appears to be closer in age to the underlying mid-Pliocene Ramsholt Member (Head, 1997).

Pollen from other Red Crag sites in eastern England (Fig. 1) provide evidence for a considerably cooler climate. The lowest 24 m of the Stradbroke borehole, Suffolk is the type section of the Pre-Ludhamian British pollen stage, and is characterized by pollen of cool, boreal affinity (Beck, Funnell & Lord, 1972). These deposits are normally magnetized, and suggest correlation with the Reuverian C of the Netherlands, although correlation with a normally magnetized

Figure 3. Dinoflagellates from the basal Walton Crag at Walton-on-the-Naze. (b–d, j) are bright field images, the others are with interference contrast. Max. dia. = maximum diameter. Various magnifications. (a, b) *Barssidinium pliocenicum* (Head). Ventral view of ventral surface, with (b) showing detail of processes. Sample WC2(1); M49/0. Central body length = 69 μm. (c) *Lejeunecysta* sp. Dorsal? view. Sample WC2(1); N8/0. Length = 48 μm. (d) *Lejeunecysta marieae* (Harland). Dorsal? view. Sample WC2(1); B54/1. Length = 30 μm. (e, f) *Tectatodinium pellitum* Wall. Ventral view at (e) mid focus, (c) of dorsal surface. Sample WC2(2); H43/2. Length = 46 μm. (g, h) *Bitectatodinium tepikiense* Wilson (columellate luxuria). (g) Uncertain view of broken specimen, upper surface. Sample WC2(2); C33/4. Dimensions = 72 x 46 μm. (h) Uncertain view of broken specimen, upper surface. Sample WC2(2); U34/0. Max. dia. = 51 μm. (i, j) *Bitectatodinium raedwaldii* Head. (i) Right dorsolateral view of upper surface. Sample WC2(1); T23/1. Max. dia. = 40 μm. (j) Uncertain view at mid focus. Sample WC2(2); F44/3. Max. dia. = 50 μm. (k) *Achomosphaera andalousiensis* Jan du Chêne, subsp. *andalousiensis*. Broken specimen with upper focus on distal process terminations, these bearing fenestrate platforms (in contrast to the perforate platforms of *A. andalousiensis suttonensis* Head, 1997). Sample WC2(2); K9/4. Max. dia. of upper platform = 22 μm. (l) *Spiniferites mirabilis* (Rossignol). Ventral view of ventral surface. Sample WC2(2); U24/1. Central body length = 42 μm.

812 m. j. head

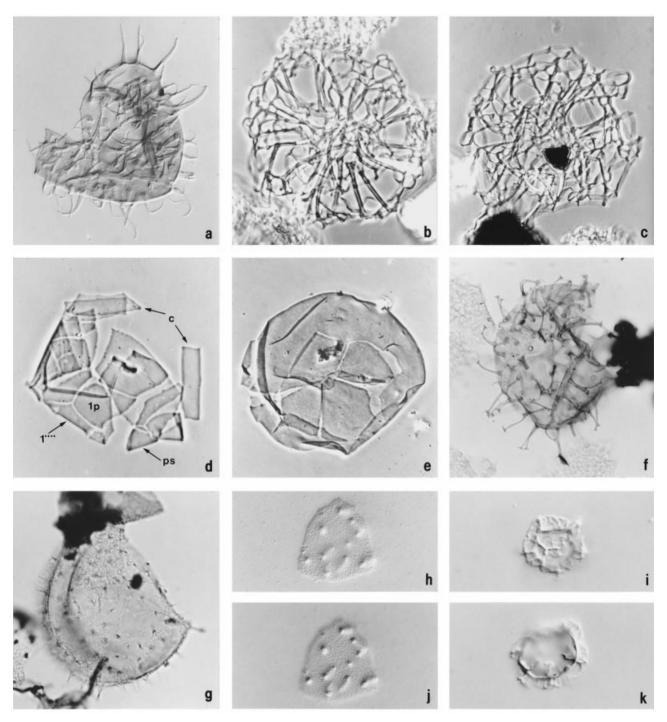


Figure 4. Dinoflagellates and an acritarch from the basal Walton Crag at Walton-on-the-Naze. (a, h–k) are interference contrast images, (b–e) are phase contrast images, and the others are in bright field. Max. dia. = maximum diameter. Various magnifications. (a) *Lingulodinium machaerophorum* (Deflandre & Cookson). Uncertain view of upper surface. Sample WC2(1); R27/3. Central body max. dia. = 51 μm. (b, c) *Nematosphaeropsis lemniscata* Bujak. Note ribbon-like trabeculae and long, uniformly-narrow process shafts. (b) Uncertain view of upper surface. Sample WC2(2); C53/0. Max. dia. including processes and trabeculae = 53 μm. (c) Uncertain view of upper surface. Sample WC2(2); S45/4. Max. dia. including processes and trabeculae = 61 μm. (d) *Geonettia* sp. of Head, 1997. Fragmented specimen bearing mostly hypocystal plates; the following plates are labelled: 1"" = antapical, 1p = posterior intercalary, ps = posterior sulcal, c = cingular. Sample WC2(2); L27/3. Max. dia. = 47 μm. (e) Gen. et sp. indet. Uncertain view of upper surface. Sample WC3; D8/4. Max. dia. = 59 μm. (f) *Operculodinium centrocarpum* sensu Wall & Dale, 1966. Uncertain view of upper surface. Sample WC2(1); S36/2. Central body max. dia. = 38 μm. (g) *Operculodinium israelianum* (Rossignol). Lateral? view of upper surface of a typical specimen, with processes about 4.5 μm long. Sample WC2(1); K49/4. Central body max. dia. = 55 μm. (h, j) *Operculodinium? eirikianum* Head, Norris & Mudie. Internal view of operculum, showing (h) upper focus and (j) slightly lower focus. Specimen has microreticulate wall surface and solid non-fibrous processes. Sample WC2(1); P7/0. Length = 21 μm. (i, k) *Cymatiosphaera? invaginata* Head, Norris & Mudie. An acritarch, probably a prasinophycean alga. Sample WC2(1); L14/0. Max. dia. including crests = 17 μm.

excursion within the Praetiglian cannot be excluded (Funnell, 1996). A similar Pre-Ludhamian assemblage has been recorded from the base of the Ormesby borehole, Norfolk, although independent correlation to the Netherlands succession was not possible (Harland et al. 1991). The Sizewell Member of the Red Crag Formation in the Aldeburgh-Sizewell area of Suffolk is normally magnetized, and contains pollen and foraminifers of Pre-Ludhamian aspect, allowing probable correlation with the Reuverian C or Praetiglian (West & Norton, 1974; Zalasiewicz et al. 1988). Although these assemblages might be assignable to the Praetiglian rather than the Reuverian C, their normal magnetization and absence of the Arctic benthic foraminifer Elphidium oregonense, which characterizes the lower part of the Praetiglian in the Netherlands (Van Voorthuysen, Toering & Zagwijn, 1972), seem to provide stronger support for a Reuverian C correlation. The Walton assemblages evidently pre-date all these assemblages.

Isolated Red Crag localities in East Anglia have yielded Walton-type molluscs, suggesting an age comparable to that of Walton-on-the-Naze. Such mollusc assemblages have been found in the lower part of the Red Crag north of the River Orwell at Brightwell and possibly as far as Boyton (Cambridge, 1977; Long & Cambridge, 1988), and perhaps also at Rothamsted (near Luton), Hertfordshire (Dines & Chatwin, 1930). No palynomorphs have yet been reported from these deposits.

Dinoflagellates of the present study cannot be compared in detail with Hunt's (1989) assemblage, which was based on just 27 specimens. However, the six specimens identified by him as *Tectatodinium pellitum* are probably misidentified, given the usual scarcity of this species (Head, 1994; Head, 1998a).

When compared to other Pliocene crag localities in eastern England, the Walton dinoflagellate assemblages have closest affinities with the Coralline Crag (Head, 1997; Table 1) but are somewhat impoverished taxonomically, probably in part because conditions were cooler. For example Capisocysta lata, an extant tropical to warm-temperate species, has been recorded both in the Coralline Crag (Head, 1998b) and the Bramertonian temperate stage of the Norwich Crag Formation (Chillesford Sand at the Chillesford Church Pit; M. J. Head, unpublished data; Fig. 1) which post-dates the Walton Crag. Yet Capisocysta has not been found at Walton. On the other hand, the cool-tolerant B. tepikiense is not known from the Coralline Crag (Head, 1997), but occurs in significant numbers at Walton. It is clear that one or more cooling events occurred after deposition of the Sudbourne member of the Coralline Crag Formation and prior to that of the Walton Crag. The following cool, Pre-Ludhamian Stage in eastern England has not been studied in any detail for dinoflagellates, but early published studies have been tentatively reinterpreted to suggest yet cooler conditions than at Walton (see Head, 1998a, for discussion). Certainly by Ludhamian times (Head, 1996) many species had disappeared from eastern England, probably reflecting Northern Hemisphere cooling at 2.55 Ma (Shackleton, Hall & Pate, 1995) and a less-equable climate that followed.

The outer neritic to oceanic extant species Nematosphaeropsis lemniscata has not been recorded in younger crag deposits of eastern England, although it occurs rarely in both the Walton and Coralline crags (Head, 1997; Head, 1998a). Its presence suggests the penetration of higher salinity North Atlantic water masses into the southern North Sea during the mid and early Late Pliocene Period, either via a postulated broad seaway linking the southern North Sea and Atlantic Ocean (Funnell, 1995)—although there is no direct evidence of such a seaway (see Hamblin et al. 1992)—or from the north via an enhanced North Atlantic Drift system associated with warmer global conditions (Dowsett et al. 1992; Dowsett, Barron & Poore, 1996; Raymo et al. 1996). Clearly more detailed and widespread investigations are necessary to assess which of these scenarios is more likely.

The Walton Crag has long been considered distinctive in comparison with other Red Crag divisions on account of its warm-water molluscan associations (Wood, 1866; Harmer, 1900a). This interpretation has since been corroborated by an abundance of the benthic foraminifer Pararotalia serrata, indicating warmtemperate conditions (Funnell & West, 1977), the absence of colder water ostracodes at Walton that occur in the younger Red Crag deposits (Lord, Horne & Robinson, 1988; Horne & Allen, 1995), and the recognition of numerous temperate species of molluscs (Meijer & Preece, 1995). But in contrast to the mid-Pliocene Coralline Crag, the Walton Crag contains an influx of cool-water species of North Pacific origins, including the marine gastropod Neptunea angulata and the benthic foraminiferan Elphidiella hannai (Funnell, 1995), and ostracode assemblages have been considered 'transitional' in their temperature affinities (Wood et al. 1993; Wood, 1996). The pollen and particularly the dinoflagellates show a similar signal of mild- to warm-temperate conditions, with some cooling having taken place after deposition of the Ramsholt Member of the Coralline Crag. The Walton Crag therefore evidently postdates the significant Northern Hemisphere cooling event at about 3.2 Ma, and precedes the next major cooling event at 2.55 Ma (Shackleton, Hall & Pate, 1995). The Walton Crag marks an important marine transgression in eastern England, and its timing (between 3.0 and 2.6 Ma) suggests a match with the third-order sea-level cycle TB3.7 of Haq, Hardenbol & Vail (1988). This cycle is likely to be glacioeustatic, apparently beginning and ending at times close to the 3.2 Ma and 2.55 Ma cooling events respectively. It is presumably this timing, between major cooling events, that helps to make the

Walton Crag assemblages so distinctive compared with other crag deposits in eastern England.

Acknowledgements. I am grateful to S. B. M. King Head (Toronto) for assistance in the field; G. Norris (University of Toronto), who provided financial support from his Natural Sciences and Engineering Research Council of Canada operating grant; S. A. G. Leroy (Queen's University, Belfast) for comments on an early version of the manuscript; and P. S. Balson (British Geological Survey, Keyworth), who generously shared his views on the sedimentology of Walton-onthe-Naze and brought my attention to some of the older literature. Reviews of the manuscript by D. J. Batten (University of Wales, Aberystwyth) and J. B. Riding (British Geological Survey, Keyworth) are greatly appreciated. It is a pleasure to acknowledge a contribution from the visitors' fund of the Geologists' Association, London.

References

- Balson, P. S. 1990. The Neogene of East Anglia a field excursion report. *Tertiary Research* 11, 179–89.
- BALSON, P. S. 1995. Sedimentary environments in the Red Crag. In *The Quaternary of the Lower Reaches of the Thames* (eds D. R. Bridgland, P. Allen and B. A. Haggart), pp. 310–11. Durham: Field Guide, Quaternary Research Association.
- Balson, P. S. 1997. The Waltonian (Late Pliocene) stratotype section at Walton-on-the-Naze, UK and the stratigraphic interpretation of cross-stratified marine deposits. Regional Committee on Northern Neogene Stratigraphy and Regional Committee on Northern Paleogene Stratigraphy, 6, Joint Biannual Meeting, Karlslunde, Denmark; Danmarks og Grønlands Geologiske Undersøgelse Rapport 1997/87, p. 8. [Abstract]
- BECK, R. B., FUNNELL, B. M. & LORD, A. R. 1972. Correlation of the Lower Pleistocene Crag at depth in Suffolk. *Geological Magazine* **109**, 137–39.
- Bell, A. 1911. On the zones of the East Anglian Crags. Journal of the Ipswich and District Field Club 3, 5–17.
- Bell, A. 1912. On the zonal stratification of the Eastern British Pliocenes. *Essex Naturalist* **16**, 289–305.
- Bell, R. G. 1887. Notes on Pliocene Beds. *Geological Magazine, Second Series* **4**, 554–8.
- Berggren, W. A., Kent, D. V., Swisher III, C. C. & Aubry, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. In *Geochronology, Time Scales and Global Stratigraphic Correlation* (eds W. A. Berggren, D. V. Kent, and J. Hardenbol), pp. 29–212. SEPM Special Publication, 54. Tulsa, Oklahoma: SEPM (Society for Sedimentary Geology).
- BOULTER, M. C. 1971. A palynological study of two of the Neogene plant beds in Derbyshire. *Bulletin of the British Museum, Natural History* **19**, 361–410.
- Bowden, D. J., Hunt, C. O. & Green, C. P. 1995. The Late Cenozoic deposits of the Naze, Walton, Essex. In *The Quaternary of the Lower Reaches of the Thames* (eds D. R. Bridgland, P. Allen and B. A. Haggart), pp. 299–309. Durham: Field Guide, Quaternary Research Association.
- BUJAK, J. P. 1984. Cenozoic dinoflagellate cysts and acritarchs from the Bering Sea and Northern North Pacific, DSDP Leg 19. *Micropaleontology* **30**, 180–212.
- CAMBRIDGE, P. G. 1977. Whatever happened to the Boytonian? A review of the marine Plio-Pleistocene of

- the southern North Sea. Bulletin of the Geological Society of Norfolk 29, 23–45.
- DALE, B. 1996. Dinoflagellate cyst ecology: modelling and geological applications. In *Palynology: Principles and Applications*, Vol. 3 (eds J. Jansonius and D. C. McGregor), pp. 1249–75. College Station, Texas: American Association of Stratigraphic Palynologists Foundation.
- DE VERTEUIL, L. 1996. Data report: Upper Cenozoic dinoflagellate cysts from the continental slope and rise off New Jersey. In *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. **150** (eds G. S. Mountain, K. G. Miller, P. Blum *et al.*), pp. 439–54. College Station, Texas: Ocean Drilling Program.
- DINES, H. G. & CHATWIN, C. P. 1930. Pliocene sandstone from Rothamsted (Hertfordshire). *Memoirs of the Geological Survey Summer Programme for 1929*, 1–7.
- DIXON, R. G. 1979. Sedimentary facies in the Red Crag (Lower Pleistocene, East Anglia). *Proceedings of the Geologists' Association* **90**, 117–32.
- DOWSETT, H. J., CRONIN, T. M., POORE, R. Z., THOMPSON, R. S., WHATLEY, R. C. & WOOD, A. M. 1992. Micropaleontological evidence for increased meridional heat transport in the North Atlantic Ocean during the Pliocene. *Science* 258, 1133–5.
- Dowsett, H. J., Barron, J. & Poore, R. 1996. Middle Pliocene sea surface temperatures: a global reconstruction. *Marine Micropaleontology* 27, 13–25.
- ELLIS, M. B. 1949. Tetraploa. The British Mycological Society, Transactions 32, 246–51.
- Funnell, B. M. 1961. The climatic and stratigraphic significance of the early Pleistocene foraminifera of the North Sea Basin. Ph.D. thesis, University of Cambridge, 325 pp. (Not seen; cited in Funnell, 1996).
- FUNNELL, B. M. 1995. Global sea-level and the (pen-)insularity of late Cenozoic Britain. In *Island Britain: a Quaternary perspective* (ed R. C. Preece), pp. 3–13. Geological Society Special Publication **96**. London: The Geological Society.
- Funnell, B. M. 1996. Plio-Pleistocene palaeogeography of the southern North Sea basin (3.75–0.60 Ma). *Quaternary Science Reviews* **15**, 391–405.
- Funnell, B. M. & West, R. G. 1977. Preglacial Pleistocene deposits of East Anglia. In *British Quaternary Studies, Recent Advances* (ed F. W. Shotton), pp. 247–65. Oxford: Clarendon Press.
- GIBBARD, P. L. & PEGLAR, S. M. 1988. Rockhall Wood,
 Sutton Pollen analysis. In *The Pliocene–Middle Pleistocene of East Anglia, Field Guide* (eds P. L. Gibbard and J. A. Zalasiewicz), pp. 71–2. Cambridge,
 U.K.: Quaternary Research Association.
- GIBBARD, P. L., WEST, R. G., ZAGWIJN, W. H., BALSON, P. S., BURGER, A. W., FUNNELL, B. M., JEFFERY, D. H., DE JONG, J., VAN KOLFSCHOTEN, T., LISTER, A. M., MEIJER, T., NORTON, P. E. P., PREECE, R. C., ROSE, J., STUART, A. J., WHITEMAN, C. A. & ZALASIEWICZ, J. A. 1991. Early and early middle Pleistocene correlations in the southern North Sea Basin. *Quaternary Science Reviews* 10, 23–52.
- HALL, C. A., Jr. 1964. Shallow-water marine climates and molluscan provinces. *Ecology* 45, 226–34.
- Hamblin, R. J. O., Crosby, A., Balson, P. S., Jones, S. M., Chadwick, R. A., Penn, I. E. & Arthur, M. J. 1992. United Kingdom offshore regional report: the geology of the English Channel. London: HMSO for the British Geological Survey, 106 pp.

- HAQ, B. U., HARDENBOL, J. & VAIL, P. R. 1988. Mesozoic and Cenozoic chronostratigraphy and cycles of sealevel change. In Sea-Level Changes—An Integrated Approach, pp. 71–108. SEPM Special Publication No. 42. Tulsa, Oklahoma: SEPM (The Society of Economic Paleontologists and Mineralogists).
- HARLAND, R. 1983. Distribution maps of Recent dinoflagellate cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. *Palaeontology* **26**, 321–87.
- HARLAND, R., BONNY, A. P., HUGHES, M. J. & MORIGI, A. N. 1991. The lower Pleistocene stratigraphy of the Ormesby Borehole, Norfolk, England. *Geological Magazine* **128**, 647–60.
- HARMER, F. W. 1900a. The Pliocene deposits of the East of England.—Part II: The crag of Essex (Waltonian) and its relation to that of Suffolk and Norfolk. *Quarterly Journal of the Geological Society, London* **56**, 705–38.
- HARMER, F. W. 1900b. On a proposed new classification of the Pliocene deposits of the East of England. *Report of the British Association for the Advancement of Science* (for 1899), 751–3.
- HEAD, M. J. 1993. Dinoflagellate cysts, sporomorphs, and other palynomorphs from the upper Pliocene St. Erth Beds of Cornwall, southwestern England. *Paleontological Society Memoir* no. 31 (*Journal of Paleontology*, 67 [3] Supplement), 62 pp.
- HEAD, M. J. 1994. Morphology and paleoenvironmental significance of the Cenozoic dinoflagellate genera *Habibacysta* and *Tectatodinium*. *Micropaleontology* **40**, 289–321
- HEAD, M. J. 1996. Paleoecological and taxonomic revision of late Cenozoic dinoflagellates from the Royal Society borehole at Ludham, eastern England. *Journal of Paleontology* **70**, 543–70.
- HEAD, M. J. 1997. Thermophilic dinoflagellate assemblages from the mid Pliocene of eastern England. *Journal of Paleontology* **71**, 165–93.
- HEAD, M. J. 1998a. Marine environmental change in the Pliocene and early Pleistocene of eastern England: the dinoflagellate evidence reviewed. *In* The Dawn of the Quaternary (eds T. Van Kolfschoten and P. L. Gibbard). *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, **60**, 199–226.
- HEAD, M. J. 1998b. New goniodomacean dinoflagellates with a compound hypotractal archeopyle from the late Cenozoic: *Capisocysta* Warny and Wrenn, emend. *Journal of Paleontology* **72**, 797–809.
- HEAD, M. J. & WESTPHAL, H. In press. Palynology and paleoenvironments of a Pliocene carbonate platform: the Clino Core, Bahamas. Journal of Paleontology.
- HORNE, D. J. & ALLEN, P. 1995. Ostracoda and Foraminifera from the Red Crag of Walton-on-the-Naze. In *The Quaternary of the Lower Reaches of the Thames, Field Guide* (eds D. R. Bridgland, P. Allen and B. A. Haggart), pp. 314–5. Durham: Quaternary Research Association.
- HUNT, C. O. 1989. The palynology and correlation of the Walton Crag (Red Crag Formation, Pliocene). *Journal of the Geological Society, London* **146**, 743–5.
- JENKINS, D. G. & HOUGHTON, S. D. 1987. Age, correlation and paleoecology of the St. Erth Beds and the Coralline Crag of England. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 24, 147–56.
- KENDALL, P. F. 1931. The Red Crag of Walton-on-the-Naze. *Geological Magazine* **68**, 405–420.
- LEWIS, J. 1988. Cysts and sediments: Gonyaulax polyedra,

- Lingulodinium machaerophorum, in Loch Creran (Scotland, UK). Journal of the Marine Biological Association of the United Kingdom 68, 701–14.
- LONG, P. E. & CAMBRIDGE, P. G. 1988. Crag mollusca: an overview. In *The Pliocene–Middle Pleistocene of East Anglia, Field Guide* (eds P. L. Gibbard and J. A. Zalasiewicz), pp. 53–6. Cambridge, U.K.: Quaternary Research Association.
- LORD, A. R., HORNE, D. J. & ROBINSON, J. E. 1988. An introductory guide to the Neogene and Quaternary of East Anglia for ostracod workers. *British Micropalaeontological Society Field Guide* No. 5, 11 pp.
- MADSEN, A. & DALE, B. 1992. Dinoflagellate cysts as indicators of eutrophication in the inner part of the Oslofjord, southern Norway. *Program and Abstracts,* 8th International Palynological Congress, Aix-en-Provence, p. 95.
- MATHERS, S. & ZALASIEWICZ, J. A. 1988. The Red Crag and Norwich Crag Formations of southern East Anglia. *Proceedings of the Geologists' Association* **99**, 261–78.
- MEIJER, T. & PREECE, R. C. 1995. Malacological evidence relating to the insularity of the British Isles during the Quaternary. In *Island Britain: a Quaternary Perspective* (ed R. C. Preece), pp. 89–110. Geological Society Special Publication no. 96. London: The Geological Society.
- MENKE, B. 1976. Pliozäne und ältestquartiäre Sporen und Pollenflora von Schleswig-Holstein. *Geologisches Jahrbuch* A **32**, 3–197.
- MORZADEC-KERFOURN, M.-T. 1977. La limite Pliocène—Pleistocène en Bretagne. *Boreas* **6**, 275–83.
- RAYMO, M. E., GRANT, B., HOROWITZ, M. & RAU, G. H. 1996. Mid-Pliocene warmth: stronger greenhouse and stronger conveyor. *Marine Micropaleontology* 27, 313–326.
- REID, P. C. 1972. Dinoflagellate cyst distribution around the British Isles. *Journal of the Marine Biological Association of the United Kingdom* **52**, 939–44.
- Reid, P. C. 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia* **25**, 579–637.
- SCHWEIZER, H.-J. 1980. Environment and climate in the early Tertiary of Spitsbergen. *Palaeogeography, Palaeoclimatology, Palaeoecology* **30**, 297–311.
- SHACKLETON, N. J., HALL, M. A. & PATE, D. 1995. Pliocene stable isotope stratigraphy of Site 846. In *Proceedings of* the Ocean Drilling Program, Scientific Results, Vol. 138 (eds N. G. Pisias, L. A. Mayer, T. R. Janecek et al.), pp. 337–55. College Station, Texas: Ocean Drilling Program.
- Sontag, E. 1966. Microbotanische (palynologische) Untersuchungen am 2. Niederlausitzer Flözhorizont. *Geologie Beiheft* **54**, 1–141.
- THIELE-PFEIFFER, H. 1980. Die Miozäne Mikroflora aus dem Braunkohlentagebau Oder bei Wackersdorf/Oberpfalz. *Palaeontographica Abt. B* **174**, 95–224.
- THOMSON, P. W. & PFLUG, H. 1953. Pollen und Sporen des mitteleuropäischen Tertiärs. *Palaeontographica, Abt. B* **94**, 1–138.
- VAN DER HAMMEN, T., WIJMSTRA, T. A. & ZAGWIJN, W. H. 1971. The floral record of the late Cenozoic of Europe. In *The late Cenozoic Glacial Ages* (ed K. K. Turekan), pp. 391–424. New Haven, London: Yale University Press.
- VAN VOORTHUYSEN, J. H., TOERING, K. & ZAGWIJN, W. H. 1972. The Plio–Pleistocene boundary in the North Sea Basin: revision of its position in the marine beds. Geologie en Mijnbouw 51, 627–39.

WALL, D. & DALE, B. 1966. 'Living fossils' in western Atlantic plankton. *Nature* **211**, 1025–6.

- Wall, D., Dale, B., Lohman, G. P. & Smith, W. K. 1977. The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic oceans and adjacent seas. *Marine Micropaleontology* 2, 121–200.
- WEST, R. G. & NORTON, P. E. P. 1974. The Icenian Crag of southeast Suffolk. *Philosophical Transactions of the Royal Society, London, Series B* 269, 1–28.
- WILSON, G. J. 1973. Palynology of the middle Pleistocene Te Piki bed, Cape Runaway, New Zealand. *New Zealand Journal of Geology and Geophysics* **16**, 345–354.
- WOOD, A. M. 1996. Pliocene Ostracoda of East Anglia (Part 1): the Walton Crag at Walton-on-the-Naze, Essex. Bulletin of the Geological Society of Norfolk 44 (for 1994), 538–52.
- Wood, A. M., Whatley, R. C., Cronin, T. M. & Holtz, T. 1993. Pliocene palaeotemperature reconstruction for the southern North Sea based on Ostracoda. *Quaternary Science Reviews* 12, 747–67.
- WOOD, S. V. 1866. On the structure of the Red Crag. Quarterly Journal of the Geological Society, London 22, 538–52.
- WRENN, J. H. & KOKINOS, J. P. 1986. Preliminary comments on Miocene through Pleistocene dinoflagellate cysts from De Soto Canyon, Gulf of Mexico. In *Papers from* the First Symposium on Neogene Dinoflagellate Cyst Biostratigraphy (eds J. H. Wrenn, S. L. Duffield and J. A. Stein), pp. 169–225. American Association of Stratigraphic Palynologists Contributions Series no. 17.
- ZAGWIJN, W. H. 1960. Aspects of the Pliocene and early Pleistocene vegetation in The Netherlands. *Mededelingen van de Geologische Stichting, Serie C–III–1*, **5**, 1–78.
- ZAGWIJN, W. H. 1974. The Pliocene–Pleistocene boundary in western and southern Europe. *Boreas* 3, 75–97.
- Zalasiewicz, J. A., Mathers, S. J., Hughes, M. J., Gibbard, P. L., Peglar, S. M., Harland, R., Nicholson, R. A., Boulton, G. S., Cambridge, P. & Wealthall, G. P. 1988. Stratigraphy and palaeoenvironments of the Red Crag and Norwich Crag formations between Aldeburgh and Sizewell, Suffolk, England. *Philosophical Transactions of the Royal Society London, Series B* 322, 221–72.

Appendix 1. Taxonomic notes on selected dinoflagellates

Barssidinium pliocenicum (Head) Head (Fig. 3a, b). Only three whole specimens were seen, although numerous fragments show a range of process morphology comparable with the type material (Head, 1993, fig. 23). Maximum central body diameter, 65, 70, and 71 μ m. Average process length, 8(9.8)13 μ m. Thirteen mostly fragmented specimens were measured

Bitectatodinium tepikiense Wilson (Fig. 3g, h). Nearly all specimens have a columellate wall structure resembling the type material from the middle Pleistocene of New Zealand (Wilson, 1973). This type material is associated with pollen that indicate a mild to warm climate (Wilson, 1973). However, a vermiculate wall pattern characterizes specimens of *B. tepikiense* found today higher latitudes of the North Atlantic. Hence the vermiculate morphotype, which is rare

at Walton, possibly reflects cooler environments than those to which the columellate morphotype is adapted. These morphotypes do intergrade in the fossil record, and careful scrutiny of both fossil and modern specimens of *B. tepikiense* will be necessary to test this possible climatic link.

Gen. et sp. indet. (Fig. 4e). A single specimen was recorded, having a smooth, thin wall. The archeopyle apparently consists of about four dislodged plates, although it has not been possible to determine their position or the orientation of the cyst. Gen. et sp. indet. bears some resemblance to Forma D of Wrenn & Kokinos (1986, pl. 10, fig. 5 only) which the authors recorded as abundant in the Pliocene and Pleistocene of the Gulf of Mexico.

Geonettia sp. of Head, 1997 (Fig. 4d). Previously known only from the mid-Pliocene Coralline Crag of eastern England (Head, 1997, 1998a, b) and upper Upper Pliocene chron C2r of DSDP Hole 603C, western North Atlantic (M. J. Head, unpublished data), this distinctive species differs from Geonettia clineae de Verteuil and Norris in its thin, smooth wall and small posterior sulcal plate. The diameter is about 38–43 μm. Fifteen specimens were found, although some are incomplete. They are readily distinguished from the related Capisocysta Warny & Wrenn by the presence of discrete cingular and epicystal plates. Work is in progress to describe this species formally.

Nematosphaeropsis lemniscata Bujak (Fig. 4b, c). The Walton specimens have broad (about 1.1–1.5 μm) ribbon-like trabeculae and long (9–14 μm), uniformly slender process shafts. All compare closely with the type material (Bujak, 1984), and with many Coralline Crag specimens (e.g. Head, 1997, fig. 16.7). A Coralline Crag variant, characterized by some proximally expanded process shafts with pronounced claustra (Head, 1997, fig. 16.8–16.10), was not found at Walton.

Operculodinium centrocarpum sensu Wall & Dale, 1966 (Fig. 4f). The central body surface is more-or-less smooth, with faint, irregularly-scattered granules. The pedium is thin (less than 0.3 µm). Processes are hollow and non-fibrous with smooth or nearly smooth shafts, and have pronounced distal platforms. Average central body diameter is 27(32.7)38 µm; average process length is 5.5(7.1)8.5 µm. Twenty-three specimens were measured. The Walton specimens compare closely with those from the Ludham borehole (Head, 1996) and Chillesford Church Beds (Head, 1994, unpublished data). The Walton specimens also strongly resemble Operculodinium? sp. of Head (1997) from the Coralline Crag which, however, may have a finely wrinkled surface under SEM (Head, 1997, fig. 16.12). Scanning electron microscope studies documenting the full range of wall detail are needed to confirm whether these two similar taxa are conspecific.

Operculodinium israelianum (Rossignol) Wall (Fig. 4g). Specimens have a fibro-reticulate luxuria. The processes are relatively short with acuminate or minutely expanded distal tips, and have an indistinctly intratabular distribution. The wall thickness is usually less than 1.0 μ m. Average central body diameter is 41(50.1)60 μ m; average process length is 2.0(3.8)7.5 μ m. Twenty-six specimens were measured from the basal horizon. The Walton specimens are similar to O. cf. israelianum from the Coralline Crag (Head, 1997), but most have shorter and less robust processes. They are probably ecophenotypic variants of the same species.

Appendix 2. Taxonomic notes on selected terrestrial palynomorphs

Nyssapollenites kruschi (Potonié) (Fig. 2l–r). A morphologically variable form-species (Thomson & Pflug, 1953). The Walton specimens are mostly prolate (e.g. Fig. 2o–r), but some are spherical, while others are oblate with circular to rounded-triangular ambs in polar view. The surface ornament varies from nearly smooth to faintly granulate and occasionally microreticulate. Some of the more conspicuously granulate specimens compare with Faguspollenites verus as illustrated by Thiele-Pfeiffer (1980, 15, figs. 4–5), although in the present study this morphotype appears to intergrade with more typical forms of N. kruschi, and so was not separately identified. The Walton specimens have a tectate wall and appear intragranulate to intramicroreticulate. Length is 25(31.1)40 μm. Seventeen specimens were measured.

Quercus-type. Specimens are generally small (length is about 19–26 μ m) and tricolpate, with a quercoid surface ornament, although some are larger (up to 33 μ m long) and others have somewhat finer ornament.

Tetracolporopollenites sapotoides Thomson & Pflug (Fig. 2k, l). A single, probably reworked specimen was recorded. This species has been reported from Miocene/Pliocene boundary age deposits in England (Boulter, 1971) and apparently does not range above the Miocene in central Europe (Thiele-Pfeiffer, 1980).

Tricolporopollenites parmularius (Potonié) (Fig. 2g, h). Specimens have a characteristic low-curvature apocolpium and a smooth, atectate wall that accepts stain poorly. Germinals vary from being clearly tricolporate (identical with Zagwijn, 1960, pl. 2, fig. 12), to tricolporoidate (Fig. 2g, h), to almost tricolpate. Length is 22–27 μm. Six specimens were measured.

Reticulataepollis pseudointergranulatus (Potonié) sensu Sontag, 1966 (reworked?) (Fig. 2i, j). A single specimen, possibly representing Viburnum, was recorded. This tricolporate species has been reported from the Miocene and possible Oligocene of central Europe (as Tricolporopollenites pseudointergranulatus Kr. in Sontag, 1966 and Thiele-Pfeiffer, 1980) and Pliocene of North Germany (as Viburnum-habitus in Menke, 1976, pl. 36, figs. 12–23 only).

818 m. j. head