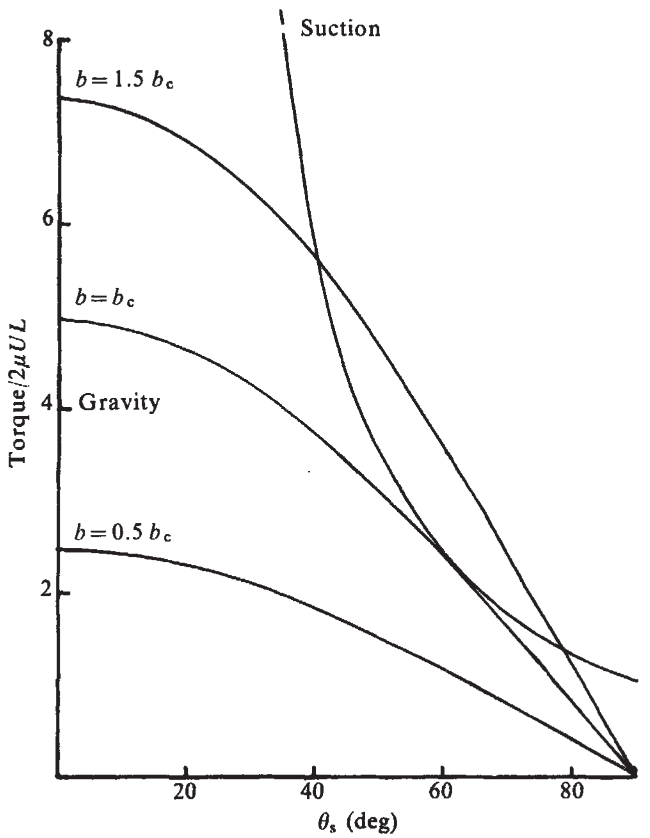

Fig. 2 The torques (in units of $2\mu UL$) as a function of subduction angle. The three cosine curves labelled by values of b are for T_G. The remaining curve is for T_H There is no solution for $T_H = T_G$ if $b < b_c$, and a solution becomes possible at $b = b_c$ when the curves just touch.

The negative buoyancy results from the thickening and cooling of the plate as the material proceeds from ridge to trench. The observed scatter of actual values for θ_s results from the inevitable interaction between several ridge and trench systems, and the inability to achieve steady-state. The following plausible values satisfy equation (4) for b_c: $\Delta\rho \sim 0.1$ g cm^{-3}, $h \sim 100$ km, $U \sim 10$ cm yr^{-1}, $L \sim 1{,}000$ km, $\mu \sim 2\times10^{22}$ P. The size of the plate depends on the time taken for plate material to achieve critical negative buoyancy and, therefore, depends on the geothermal heat flux. This dependence may help to explain why plate tectonics was apparently so different in the Precambrian[14].

The model we present here is oversimplified and incomplete, but it illustrates how the general physical principles of subduction dynamics might be identified. The choice of model is best made by comparing different tectonic systems, and data on the plate tectonics for the Earth at a different epoch or for other planets is essential for future progress.

After this work had been completed, the very closely related calculations by Tovish *et al.*[15] were brought to our attention.

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Age and tectonic implications of the Baie d'Audierne basic-ultrabasic complex

Major deformational and metamorphic events in the south-armorican metamorphic belt of south Brittany have been considered to be either Cadomian and Variscan[1] or Ordo-Silurian (Ligerian) and Variscan[2] in age. Geological interest in southern Brittany is, at least in part, focused upon the blue-schists[3] and the basic–ultrabasic complexes of the area. The largest of these basic–ultrabasic complexes is that of the Baie d'Audierne group (Fig. 1). Although lacking suitable material for direct radiometric or stratigraphical dating, several indirect attempts have been made to date this group, using field data. These are briefly outlined here. It is proposed that the deformational and metamorphic history of this complex is entirely Variscan in age. The implications of this conclusion for the recently proposed plate-tectonic model of Cogné[2] are discussed.

The south-armorican metamorphic belt comprises a suite of non-fossiliferous, pre-Stephanian sediments, commonly ascribed to the late Proterozoic Brioverian[4], which have been folded, metamorphosed and intruded by basic and ultrabasic rocks, granites and granite gneisses[5,6]. In the Baie d'Audierne region (Fig. 1), two divisions within the metamorphic rocks, an upper and a lower suite separated by an unconformity have been recognised[7–9]. It is thought that the lower suite was folded and metamorphosed in the amphibolite facies (kyanite grade) during the late Proterozoic Cadomian orogeny[8] before the deposition of the upper suite. The upper suite commenced with the deposition of a basal sedimentary series, the Languidou gneiss. Ordovician to Carboniferous sediments lie offshore of the Baie d'Audierne; their relationships to the upper suite is, however, uncertain[9]. In the Baie d'Audierne, the upper suite is cut by the Pors Poulhan granite gneiss (Fig. 1) which has yielded a whole rock Rb/Sr isochron at 334 ± 8 Myr (λ^{87}Rb $= 1.47\ 10^{-11}$ yr^{-1}). This radiometric date has been interpreted as the magmatic cooling age of the granite. Subsequently, the whole sequence, upper and lower suites and the intruded Pors Poulhan granite, was folded by upright folds on east–west axes and metamorphosed in the albite–amphibolite facies during the Variscan orogeny[8]. Late Variscan granites intrude all the metamorphic rocks and are probably associated with other south-armorican granites emplaced into rocks of Upper and Lower Palaeozoic age[11].

During recently completed fieldwork in the area where Cogné and Peucat defined the upper and lower Brioverian, in the Baie d'Audierne region (Fig. 1), I was unable to recognise any unconformity. The upper and lower suites throughout the area show a common structural and metamorphic history. In addition, the Languidou gneiss, interpreted by Cogné[7] as a metaconglomerate and used by Peucat[8] to support the postulated unconformity, is thought to be an intrusive granite containing partially assimilated xenoliths of country rock. The supposed 'pebbles' are deformed feldspar porphyroblasts and quartz–feldspar segregations. The Languidou gneiss shows the same pre-tectonic relationship to the surrounding metasediments as the Pors Poulhan gneiss. This pre-tectonic relationship also applies to an association of gabbro and peridodite (now amphibolite, garnet–pyroxenite and serpentinite, ascribed by Peucat to his lower suite) which intrude the metasediments. Following the intrusion of these ultrabasic to granitic rocks, the entire complex (the Baie d'Audierne group[6]) was isoclinally folded and metamorphosed in the amphibolite facies, up to sillimanite grade, with the development of an axial planar schistosity. This early schistosity was deformed by rare isoclinal folds and

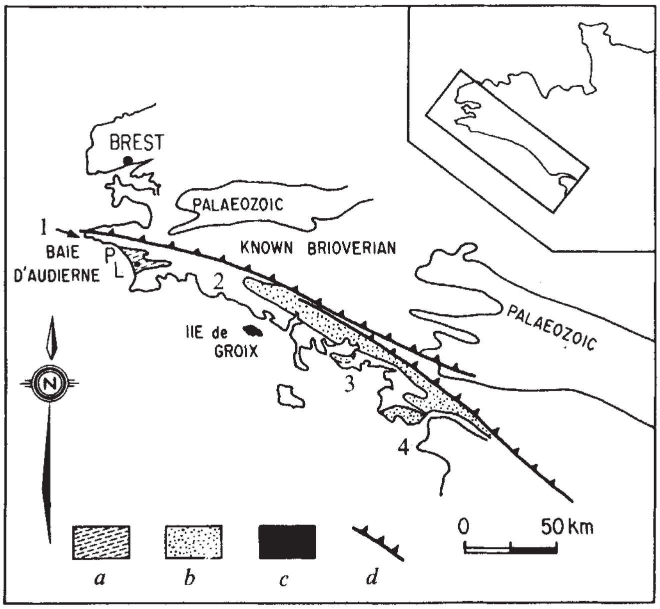

Fig. 1 Present-day distribution of the Baie d'Audierne group (*a*), south Brittany migmatites, (*b*) the Ile de Groix blueschists (*c*) and the spatial relationship to the Brioverian and Palaeozoic sediments north of the South Armorican Shear Zone (*d*); the blueschists may originally have been more widely separated from the mainland migmatites as they are bounded north and south by faults, possibly thrusts[24]. L, Languidou; P, Pors-Poulhan. 1, Cap Sizun gneisses; 2, Port Manech gneiss; 3, Morbihan; 4, Basse Loire (After Cogné[1]).

these in turn are refolded by upright folds on east–west axes, with a variably developed associated crenulation cleavage. The complex then underwent a mimetic annealing recrystallisation which did not produce any major retrogression of the earlier mineral assemblages. A subsequent retrogression in the greenschist facies is associated with the emplacement of the latest Variscan granites. A fuller account of the Baie d'Audierne area is given elsewhere[6].

Similarly, the structural discordance representing the lateral extension of the unconformity within the metasediments of the metamorphic belt south of the South Amorican Shear Zone has been observed neither in Morbihan[12] nor Basse Loire[13] (Fig. 1). From the above model, all the structural and metamorphic events affecting the rocks of the Baie d'Audierne group occurred between the emplacement of the Pors Poulhan gneiss and that of the late Variscan granites. If we accept the 334 ± 8 Myr age given by the Pors Poulhan gneiss as an emplacement age, then the folding and metamorphism in the Baie d'Audierne area must have occurred entirely within the Upper Palaeozoic and forms part of the Variscan orogeny.

To the east, south east of the Baie d'Audierne, a suite of migmatites and anatectic granites outcrops (Fig. 1), within which the anatectic granite represents the culmination of migmatisation[1]. To the south of the migmatites, metamorphic rocks of the blueschist (glaucophane–lawsonite) facies outcrop on the Ile de Groix[3,14,15]. The anatectic granites have yielded a whole rock Rb/Sr isochron at 363 ± 12 (λ^{87} Rb $= 1.47\times10^{-11}$ yr^{-1}) (ref. 16). A premigmatisation orthogneiss (Roguedas) has yielded a Rb/Sr whole rock isochron age at 460 Myr (λ^{87} Rb $= 1.42.10^{-11}$ yr^{-1}) (ref. 17), so fixing the migmatisation between 460 Myr and 363 Myr. The diapiric rise of the anatectic granites is syn-second phase deformation in the surrounding migmatities[18]. This, in conjunction with the radiometric data, suggests the presence of a polyphase history of pre-Variscan[2], high temperature metamorphism and deformation to the east whose early events and climax are older than the proposed post-334 Myr orogenic activity in the Baie d'Audierne to the west.

The radiometric ages for the migmatite suite are broadly similar to those for the time range of blueschist metamorphism on the Ile de Groix (420–370 Myr) (ref. 17) as inferred from Rb/Sr mineral and whole rock data (λ^{87} Rb $= 1.42.10^{-11}$ yr^{-1}). A K/Ar 335 Myr mineral age has been suggested for this blueschist metamorphism[19], which may, however, represent a later thermal event. In view of the spatial association of the above mentioned radiometric ages, rock types and metamorphic facies, it is possible to place the rocks of the Baie d'Audierne within the context of recently proposed tectonic models for south Brittany[2,20]. Such a tectonic context is necessarily confined to the south of the South Armorican Shear Zone due to the uncertainty concerning the movement history on this major tectonic line (P. Jegouzo, personal communication) and, therefore, the questionable validity of direct correlation between the south amorican metamorphic belt and central or north Brittany, the British Isles and so on.

The dominant strike trend in the Baie d'Audierne region is 070° (ref. 6); that of the migmatite belt to the east–south east is 110–120° (ref. 1). A gently curved arc can be envisaged, truncated by the late Variscan granites and mylonites of the South Armorican Shear Zone. Before the emplacement of these granites and the subsequent shear zone movement, the Baie d'Audierne group, which extends westwards to the edge of the submarine continental shelf[9], would have extended to the east–north east, around the northern flank of the migmatite belt (Fig. 2). Whether or not the migmatite belt extended south of the present outcrop of the Baie d'Audierne group cannot be ascertained, as this position is occupied by a large, late Variscan granite (Pont l'Abbé). It is with this pre-late Variscan granite configuration in mind that the tectonic significance of the Baie d'Audierne group is discussed.

At, or even before, ~420 Myr ago, blueschist metamorphism was taking place to the south of a high temperature–medium

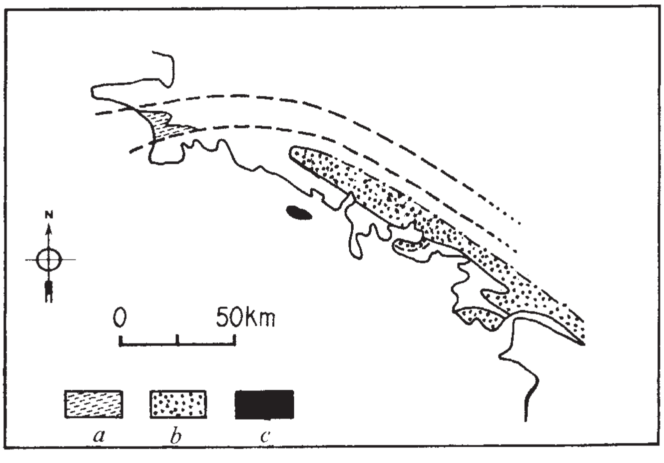

Fig. 2 Proposed configuration of rocks of Baie d'Audierne (*a*), Migmatite Belt (*b*) and Ile de Groix blueschist (*c*) types pre-emplacement of the late Variscan granites.The true location and lateral extent of (*c*) cannot be ascertained[24]. Dashed lines indicate suggested boundaries.

pressure belt within which anatexis eventually occurred[2]. Relict areas of older granitic material (Port Manech and Cap Sizun gneisses) within the western part of the high temperature zone[1,6,17] suggest that the migmatite belt lay on, or immediately to the south of, continental crust (Fig. 3). The metamorphic belt therefore comprised an Andean type margin with a northward dipping subduction zone[2,20].

Metamorphism and deformation of this margin during the Ordo–Silurian (Ligerian) orogeny[3] was related to subduction and the eventual arrival of northward moving continental material (Fig. 3), now lying immediately south of the blueschists (micaschists, granites and undifferentiated Palaeozoic sediments of the South Brittany continental shelf[2,21]. In the Baie d'Audierne area, sometime between the initiation of subduction (~420 Myr) and 334 Myr ago, rifting occurred

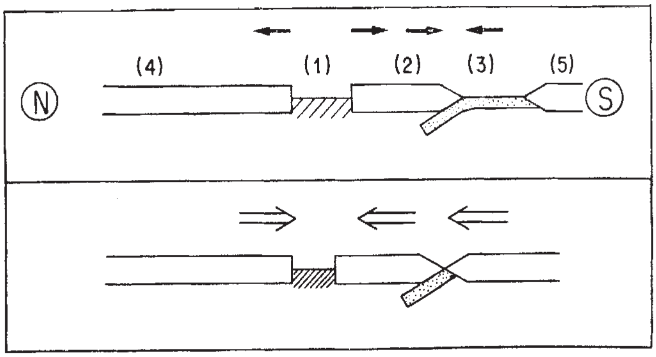

Fig. 3 Non-scaled diagram of postulated plate boundary relationships during the Palaeozoic, representing an hypothetical approximately north–south cross section across Fig. 2: 1, Baie d'Audierne type basic and ultrabasic rocks; 2, south Brittany migmatites; 3, Ile de Groix blueschists associated with oceanic crust; 4, northern continental block; 5, southern continental block. Post-420 Myr/pre-334 Myr plate motions (solid arrows) involve northward subduction at the southern margin of the migmatitic island arc (2), behind-arc extension (1) and northward movement of the southern continental block. Post-334 Myr, the behind-arc rift closes (open arrows, as the island arc + southern continent (2+5) collide with the northern continental block (4). (Adapted after Cogné[2]).

within the continental plate just to the north of the migmatite belt (Fig. 3). Into this rift, mantle derived gabbro and peridotite were intruded, representing the initial stages in the development of a marginal basin behind an island arc[22], now deeply eroded and represented by the migmatite belt. (A mid-ocean ridge origin for these basic and ultrabasic rocks has also been suggested[8,23].)

At or post ~334 Myr ago, the migmatitic island arc, then in contact with the southern continental block (Fig. 3), was pushed northwards against the northern continental block, folding the behind arc rift zone and producing the Variscan deformation and metamorphism seen in the Baie d'Audierne. This continent plus island arc–continent collision corresponds to Cogné's intercontinental collision of the same age[2]. In Cogné's model, however, the 'suture' representing this collision is marked by the South Armorican Shear Zone to the north (Fig. 1).

The south-armorican metamorphic belt was situated therefore, at an active Andean type continental margin about 420 Myr ago, which after passing through a phase of back-arc rifting, progressed to a collision with a southern continent plus island arc and the northern continent, post 334 Myr ago.

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Spike responses of 'non-spiking' visual interneurone

Our understanding of information processing in nerve nets has been modified by the concept of graded signal transmission[1]. Descriptions of non-spiking interneurones in insects[2–8], and the demonstration of graded synaptic transmission[3] have contributed to this development. In the fly visual nervous system, second and higher order interneurones are known, which apparently do not produce action potentials[6–8]. We show here that at least eight individually identifiable movement-sensitive cells, which have the characteristic properties of non-spiking interneurones[2] will generate spikes with imposed hyperpolarisation. Their graded mode of operation is due to maintained refractoriness. This applies selectively to neurones, which belong to either of two anatomically, and physiologically distinct classes. Other cell types in the same preparation generate spikes spontaneously.

The third visual neuropil of flies contains two conspicuous sets of directionally-selective movement-sensitive neurones[9,10]—an array of 10 'vertical cells' (VS 1–VS 10) which respond to vertical movements in the ipsilateral visual field, and an array of three 'horizontal cells' (HS 1–HS 3) which respond to horizontal rotary movements in the visual field of the two eyes[7,8]. Figure 2*a–f* shows some of the characteristic responses to visual stimuli of the neurone VS 1 depicted in Fig. 1. Its membrane potential in the dark is about –41 mV, modulated by sparse synaptic activity (Fig. 2*a*). Illumination of the receptive field causes a small depolarisation and a marked increase in 'noise' (Fig. 2*b*). When a striped pattern moves upwards in the receptive field, the cell is hyperpolarised, and the noise reduced (Fig. 2*c*). With downward movements it is depolarised, and the noise increased (Fig. 2*d*). Clockwise (Fig. 2*e*). or counterclockwise (Fig. 2*f*) horizontal movements are ineffective. The movement responses are largest at a pattern speed of 2 periods per s, thus corresponding to the velocity-dependent optomotor behaviour of intact flies[11–13]. It is possible to record this kind of electrical activity from any one of the VS- or HS-cells for more than 1 h, without ever

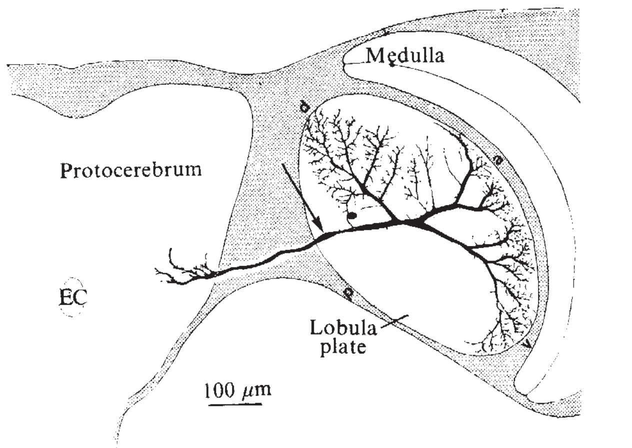

Fig. 1 Neurone VS1 of the blowfly *Calliphora erythrocephala*, as reconstructed after procion yellow injection, and serial sectioning. The right half of the fly's brain is shown from behind. Neuropil areas are white, tracts and perikaryon layers are shaded. The retinotopic projection of the ipsilateral visual field into the plane of the third visual neuropil (lobula plate) is indicated. VS1 belongs to a set of 10 large movement sensitive neurones, which occupy the caudal face of the neuropil. Their dendritic arborisations are in the lobula plate, the somata are in the caudal surface layer, and their axon terminals are close to the oesophageal canal (EC). Field axes: a–p, antero-posterior (horizontal); d–v, dorsoventral (vertical); arrow: site of penetration.