Chapter 1 – Introduction and objectives

“Plesiosaurus! A fresh-water Plesiosaurus!’ cried Summerlee. ‘That I should have lived to see such a sight! We are blessed, my dear Challenger, above all zoologists since the world began!’”

“The Lost World”
Arthur Conan Doyle, 1912

“...A remarkable deviation from all known recent and fossil reptiles…the Plesiosaurus might be compared to a serpent threaded through the shell of a turtle”

“The Medals of Creation”
Gideon Mantell, 1844

1.1. General Introduction

Plesiosaurs are a group of secondarily aquatic diapsid reptiles belonging to the clade Sauropterygia (Carroll, 1988). Diapsids (subclass Diapsida) are a monophyletic group supported by both morphological and molecular data (Lee, 2001) including lizards, snakes, crocodiles and birds, and represent a major sub-group of the amniote vertebrates, i.e. vertebrate organisms with the ability to lay eggs on land (Benton, 1997). The Sauropterygia, as a subgroup of this lineage, includes plesiosaurs, nothosaurs, pachypleurosaurs, and placodonts, taxa in which there is a single pair of temporal fenestrae at the rear of the skull, as opposed to two pairs in most other diapsids (Figure 1.1): this modified diapsid condition is known as euryapsid and is shared with ichthyosaurs. The Euryapsida is variously considered a monophyletic taxon within diapsids (e.g. Caldwell, 1996), or as a recognised (Benton, 1997) or unrecognised (Müller, 2003) polyphyletic assemblage. Plesiosaurs were predominantly marine organisms, although their fossils are not uncommon in brackish, or even freshwater deposits (Cruickshank, 1997; Sato et al. 2002). In terms of their general palaeobiology, all plesiosaurs were carnivorous, ranging in ecological strategy from piscivores and cephalopod catchers (Martill, 1992; Sato and Tanabe, 1998), to super-predators capable of subduing other large marine reptiles (Massare, 1987; Thulborn and Turner, 1993). There is also inferred and direct evidence that plesiosaurs may have occasionally ingested shelled benthic organisms (McHenry et al. 2005). Plesiosaurs vary in size from around 1.5m long (e.g. Thalassiodracon from the Lower Lias of the UK, 205 million years ago [Ma] [Figure 3.12]) to 15m long giants (e.g. Pliosaurus from the Middle Jurassic Oxford Clay Formation of the UK, 149-159 Ma) (e.g. Buchy et al. 2003). Isolated remains, including a 3m long mandible
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Figure 1.1. Diagrams of the four main types of temporal organisation in amniote skulls. A. anapsid (no temporal fenestrae), B. synapsid (single lower temporal fenestra), C. diapsid (two temporal fenestra, upper and lower), D. euryapsid (single upper temporal fenestra). Plesiosaurs possess the euryapsid condition (see text for discussion) (modified from Benton, 1997).

Figure 1.2. Cladogram showing the broad-scale interrelationships amongst basal sauropterygians indicating the derived position of Plesiosauria within the clade (arrow) (modified from Rieppel, 2000).
(Tarlow, 1959; Noè et al. 2004) indicate that these animals perhaps exceeded 17m in length (McHenry et al. 1996; Creisler, 1998). Despite their familiarity to the public and vertebrate palaeontologists alike, many aspects of the biology and evolutionary history of these marine reptiles remain poorly understood.

Plesiosaurs have an extensive fossil record: they are known from definite but non-diagnostic material from as early as the Middle Triassic, 228-245 Ma (see Benton, 1993 and references therein) but the oldest diagnostic specimens originate from the latest Triassic, 205 Ma (Taylor and Cruickshank 1993; Storrs, 1994). The fossil record shows that plesiosaurs radiated rapidly and reached a cosmopolitan distribution by the early Jurassic around 170 Ma. Subsequent to this radiation, they did not deviate far from a basic structural and adaptive framework (e.g O'Keefe, 2002). Their greatest diversity was achieved in the Late Jurassic (Sullivan, 1987) and as a group they persisted through a number of Mesozoic extinction events (Bakker, 1993), finally becoming victims of the Cretaceous-Paleogene (K-P) mass extinction (65.5 Ma) that claimed so many other large aquatic and terrestrial vertebrate groups (Sullivan, 1987; Bardet, 1994, 1995).

Plesiosaur ancestry has been firmly placed amongst basal sauropterygians (see Rieppel, 2000 and refs therein) (Figure 1.2). In 1914, Williston wrote:

“They began their career as fully evolved plesiosaurs, so far as we know, near the close of the Triassic period”.

However, there has been a recent surge in the number of taxa possessing a mosaic of basal sauropterygian and derived plesiosaurian characteristics, and this makes distinguishing and defining plesiosaurs all the more difficult. On the plus side, this aids phylogenetic analyses as more and more closely related forms are discovered and described. Traditionally, the pistosaurid Pistosaurus is regarded as the sister taxon to all plesiosaurs (Sues, 1987). The recently identified pistosauroid taxa Augustasaurus hagdorni Sander et al. 1997, Bobosaurus forojuliensis Dalla Vecchia, 2006, and Yunguisaurus liae Cheng et al. 2006, possess a number of derived characters associated with plesiosaurs, and so these taxa provide interesting information regarding the origin of plesiosaurs. In addition to providing new anatomical data, the age and location of these taxa have important implications for understanding the timing of plesiosaur origins: Yunguisaurus is from the Carnian (early Late Triassic) of China (Cheng et al. 2006), Bobosaurus is from the Carnian of
Italy (Dalla Vecchia, 2006), *Augustasaurus* is from the Anisian (Middle Triassic) of the USA (Sander et al. 1997), and *Pistosaurus* is from the Anisian of Germany (Sues, 1987) and similar remains have been described from the Rhetian/Hettangian of the UK (Cruickshank, 1996a). These plesiosaur-like semi-aquatic sauropterygians are distributed worldwide in rocks deposited millions of years before the first known diagnostic plesiosaur. Because this thesis concerns some of the oldest known diagnostic plesiosaur taxa, these pistosauroid taxa are particularly pertinent to this study.

Within Plesiosauria as currently defined (O'Keefe, 2001a), there are two generalised morphotypes: pliosauromorphs with large heads and short necks, and plesiosauromorphs with small heads and long necks (O'Keefe, 2002) (Figure 1.3). Although the gross morphology of the plesiosaurian postcrania is widely considered to have been anatomically conservative throughout the evolution of the group (Carroll, 1988; Storrs 1999), this is actually unsubstantiated and may reflect a relative lack of research on plesiosaur postcrania. There are some plesiosaur taxa, including those forming the basis of this thesis, which do not fit neatly into either of these traditional morphotypes. The large pliosaur *Rhomaleosaurus* (Chapters 3 and 4) for example, possesses a long neck and a large head; these early forms are therefore potentially pivotal in understanding the evolution and significance of plesiosaur morphotypes.

### 1.2 Palaeobiological review

The function of the relatively long neck in plesiosaurs, their most famous characteristic, is unresolved (Storrs, 1993; Ellis, 2003); that it was a successful adaptation is demonstrated by its duration throughout the long evolutionary history of the clade (Noè, 2006). Contrary to suggestions by early workers such as Zarnik (1925) who suggested the long neck was flexible and acted like a ‘harpoon’, the flexibility of the plesiosaur neck was in fact quite limited due to the close and rigid articulation between successive cervical vertebrae (Evans, pers. comm. and pers. obs.). Therefore the neck could not coil up to allow the animal to strike prey in the manner of a snake or pleurodiran turtle (Pough *et al.* 1996). In fact, the neck most likely served as a mechanism for approaching prey, say a school of fish, without the large body of the plesiosaur being detected (Massare, 1988; Ellis, 2003). It has also recently been suggested that the long neck may have been an adaptation for bottom feeding (Noè, 2006; Buchy, 2005).
Figure 1.3. Life restorations of plesiosaurs. A. A typical plesiosaurotomorph (*Elasmosaurus platyurus*), B. a typical pliosauromorph (*Liopleurodon ferox*).
A fully aquatic existence presents problems for egg-laying reptiles because they must make nests on land. Plesiosaurs, however, almost certainly overcame this problem by evolving viviparity (the ability to give birth to live young), as has been documented for other major groups of aquatic reptiles: ichthyosaurs (summarised by Benton, 1991) and mosasauroids (Caldwell and Lee, 2001). Gravid mothers and isolated embryos are known amongst basal sauropsyrgians (nothosaurs and pachypleurosaurs) (Cheng et al. 2004; Renesto et al. 2003) indicating viviparity in these taxa; thus by applying a behavioral ‘phylogenetic bracket’ (Witmer, 1995) to Sauropterygia as a whole, plesiosaurs were probably also viviparous. Unfortunately no fossil embryos have been described to empirically verify this behavior in plesiosaurs. Recently, however, Everhart (2007 p.103) points out that some undescribed plesiosaur material represents “fossils of unborn young have been found inside a mother’s body cavity”, providing the first solid evidence for this conjecture. Fossil plesiosaur embryos were also once identified by Seeley (1896), but they were later re-identified as nodular shrimp burrows (Thulborn, 1982).

A specialised underwater olfactory system has been suggested as a common adaptation in the Plesiosauria (Cruickshank et al. 1991, Brown and Cruickshank, 1994). The internal nostrils - or choanae - are situated anteriorly on the palate and are sometimes associated with palatal grooves, which have been interpreted as adaptations to channel water into the internal nares (Cruickshank et al. 1991). The flow of water through the nasal passage would thus have been maintained by hydrodynamic pressure over the retracted external nares during locomotion, and during its passage through the nasal ducts water would have been ‘tasted’ by olfactory epithelia. Consequently, under this scenario, the nares had no likely role in air intake and inhalation would have been accomplished via the mouth only. However, this long standing model was recently challenged (Buchy et al. 2006), and an alternative interpretation of the palate was proposed in which the choanae are re-identified at the rear of the palate (i.e. in this interpretation, the choanae are identified as the openings traditionally regarded as posterior interpterygoid vacuities), with the openings traditionally regarded as choanae in plesiosaurs being re-identified as vacuities associated with salt excreting glands. If this is the case, then the external nares may indeed have served a role in breathing at the water surface, as suggested by some early workers (e.g. Zarnik, 1925). More well-preserved fossil specimens will be required to resolve this debate. The traditional terminology for the internal nares is applied throughout this thesis.
Plesiosaurs are known to have intentionally swallowed stones (Taylor, 1981, 1993) - gastroliths are commonly preserved in the abdominal region of both plesiosauroids (Ellis, 2003; Everhart, 2005) and pliosauroids (Martill, 1992; Taylor, 1992b). When present, these gastroliths are usually found in quite small numbers although concentrations of more than six hundred are known for some elasmosaurid specimens (Everhart, 2005). These stones may have been used for grinding food in the stomach or may have had a role in buoyancy control (Taylor, 1993), offering a less physiologically expensive way of attaining negative buoyancy than pachyostosis (the production of thickened or dense bone). Although pachyostosis is rare amongst plesiosaurs (it is common in basal sauropterygians [Rieppel, 2000]), it is present in the ribs of the genus *Pachycostasaurus* from the Middle Jurassic Oxford Clay Formation of England (Cruickshank *et al.* 1996), and in the ribs of *Kronosaurus boyacensis*, from the Aptian (Lower Cretaceous) of Colombia (Hampe, 1992). More recently, Henderson (2006) conducted a computational study of the effects of gastroliths in plesiosaurs and showed that rather than effecting buoyancy the presence of these stones would have increased stability and equilibrium of the body in water. Gastroliths may, of course, have had a dual or even multi-purpose in these animals.

### 1.3 Locomotion

All plesiosaurs are derived with respect to basal sauropterygians (i.e. placodonts, nothosaurs and pachypleurosaur) in the acquisition of four hydrofoil-shaped flippers, a shortened trunk, and large plate-like limb girdles (Sues, 1987) (Figure 1.4). The ventrally expanded plate-like pectoral and pelvic girdles, together with the closely packed and well-formed 'gastral basket' and tightly articulated spine provided a sturdy base for movement of the four hydrofoil-shaped flippers; these adaptations reflect a shift from an axial to a paraxial lift-based locomotory repertoire (Robinson 1975; Storrs 1993). There was only one mobile joint in the plesiosaur limb (i.e. the glenoid/acetabulum) and the fifth digit is shifted proximally relative to the other digits, serving to reduce flexibility and maintain a stiff limb or 'wingfin' (Adams, 1997) (Figure 1.4). The precise function of these wingfins is uncertain; because plesiosaurs are extinct they cannot be subject to experimental hydrodynamic study. Watson (1924) interpreted plesiosaurs as rowers with their limbs functioning as oars, providing a strong backstroke coupled with a feathered recovery stroke. However, this model was subsequently discounted by Robinson (1975) using a number of clear lines of evidence – particularly the construction of the glenoid and the acetabulum (the only moveable limb joints in plesiosaurs), and the ‘wing-like’, rather than ‘oar-
Figure 1.4. Outline of *Rhomaleosaurus victor*, a plesiosaur from the Posidonia Shale of Germany, exposed in ventral view showing the plate-like girdles, tightly packed gastralia and wing-like limbs, typical of all plesiosaurs (length = 3.44m).
like’, shape of the limbs. Rowing – moving the limbs back and forth as four flat plates – would generate little useful lift, only turbulence (Katz and Plotkin, 1991). Plesiosaur limbs are certainly efficient for underwater flying, with tapered tips for reducing drag (Storrs, 1993), and so the rowing model was replaced with an ‘underwater flying’ scenario. Godfrey (1984) updated the model and suggested a repertoire now known as ‘rowing flight’ (Riess and Frey, 1991). In this model, plesiosaurs employed a modified form of flying combining principles of both rowing and flying, in which the downstroke provides both thrust and lift, and the feathered recovery stroke is more-or-less passive. Locomotion is still a poorly understood and actively researched area of plesiosaur palaeobiology. The main area of uncertainty stems from the unique plesiosaur bauplan – they are the only known vertebrate organisms possessing two pairs of fins with a function in propulsion – this raises the question of how these limbs moved relative to each other: the so-called ‘four wing problem’ (Halstead, 1989). The pectoral and pelvic girdles of plesiosaurs are predominantly reinforced ventrally for muscle attachment to enable a very powerful downstroke but only a weak upstroke (Godfrey, 1984). It has been proposed that the fore and hind limbs alternated to compensate for the lack of thrust during the weak upstroke of one pair of limbs (i.e. the other pair would provide the thrust) (Frey and Riess, 1982; Riess and Frey 1991). Hypothetically, this could provide efficient and constant forward motion. Lingham-Solier (2000) regards the rear limbs as being of little or no use in a flying propulsive locomotion, instead being used only for steering and stability while Sanders et al. (2004) endorse a repertoire in which all four flippers move in synchrony. Recent research into the efficiency of these different models using robots, suggests that these repertoires may have been interchangeable and depended on the specific speed and manoeuvrability desired by the animal (Long et al. 2006). Short bursts of speed would have been possible by combining the down stroke of both pairs of limbs simultaneously. Indeed, extant animal are known to change gaits in relation to speed and muscle efficiency (minimising energy output) (Rayner, 2003). Gait may have varied between taxa too, for example, pliosauroomorph plesiosaurs have been interpreted as more rapid and manoeuvrable swimmers than other plesiosaurs (Robinson 1975; Massare, 1988. O’Keefe, 2001b).

The ability of plesiosaurs to move on land is another point of contention (Ellis, 2003). The mechanics of their skeletons imply a completely aquatic existence: the limb girdles are only weakly connected to the axial skeleton and this would inhibit the transfer of force from limbstrokes into movement on land. However, small plesiosaurs
may have been relatively unaffected by these constraints and might have used their powerful limb downstrokes to propel themselves forward in short ‘hops’.

1.4 Anatomy

There is huge variation in the size and shape of plesiosaur skulls, but the general structure remains consistent throughout this clade (Figure 1.5). The parietals form a midline crest situated between the single pair of large upper temporal fenestrae and a pineal foramen is usually present at the anterior border of the parietal. In life, this foramen would have contained a light-sensitive pineal organ. The external nares are small and retracted close to a pair of large upward-facing orbits. The internal nares of the secondary bony palate are situated anteriorly and there is always a pair of posterior interpterygoid vacuities at the rear of the palate, exposing the braincase. An anterior interpterygoid vacuity between the pterygoids may, or may not, be present depending on taxa. The jaw articulation is formed by the quadrate (the quadratojugal is lost) and by the articular. All plesiosaurs possessed pointed teeth set in individual sockets, in life these were constantly replaced. Plesiosaur dentition consists of uniform long and conical teeth with longitudinal ridges (Figure 1.5A), but there is great variation within this typical situation. On one extreme some plesiosaurs had hundreds of tiny smooth pin-like teeth (Cruickshank and Fordyce, 2002) (Figure 1.5B) while on the other some had large robust coarsely ridged teeth (Tarlo, 1960) (Figure 1.5C).

A pair of nutritive foramina (or foramina subcentralia) are situated on the ventral surface of each vertebral centrum. This conspicuous character is one of the easiest to help identify isolated fossil plesiosaur vertebrae. In the cervical vertebrae, each lateral surface of each centrum bears an articulation for a cervical rib: these are double-faceted in early and most primitive plesiosaurs, but this number is reduced to a single facet in later and more derived forms (Persson, 1963). In the anterior cervical centra, the ribs are borne on the ventro-lateral surface of the centrum, but the rib facets migrate dorsally in the more posteriorly situated vertebrae. The cervical series merges into a transitional series of ‘pectoral’ vertebrae into the dorsal series. During this transition the rib facets migrate from the centrum onto the neural arch where they become long transverse processes in the dorsal vertebrae. These processes support long dorsal ribs. The dorsal centra are often distinctly spool shaped so that the lateral and ventral surfaces are concave. From the dorsal series we pass through the sacral and caudal series, where the rib facets return to the
Figure 1.5. Variation in plesiosaur skulls and dentition. A. *Hydorion brachypterygius*, a plesiosaurid from the Toarcian of Germany (Based on Brown, 1993). B. *Kaiwhekea katiki*, a cryptoclidid from the Maastrichtian of New Zealand (Redrawn from Cruickshank and Fordyce, 2002). C. *Lio-pleurodon ferox*, a pliosaurid from the Callovian of Europe. Redrawn from Noë *et al.* (2003) (Scale bar = 10cm).
centrum. The caudal vertebrae also bear facets for chevrons on their ventral surfaces.

The pectoral and pelvic girdles of plesiosaurs are expanded ventrally into plates (Figure 1.4). The main elements in the pectoral girdle are the coracoids and the scapulae - where these meet on their lateral surfaces they form a laterally facing glenoid facet to accommodate the forelimb. Situated between the scapulae are the clavicles and the interclavicle. In the pelvic girdle, the acetabulum is formed by the pubis situated anteriorly and the ischium posteriorly. The ilium in plesiosaurs is a small rod-like element bridging the gap between the sacral ribs and the pelvic girdle - it only contacts the ischium, another diagnostic characteristic for all plesiosaurs (Sues, 1987). Between the girdles is a mesh of gastralia (the ‘gastral basket’ or ‘plastron’); this structure consists of a central row of more-or-less symmetrical median ribs and a number of overlapping lateral ribs (Figure 1.4).

Both the fore and hind limbs of plesiosaurs are developed into wing-like flippers, which closely resemble each other. The propodials (humerus/femur) are relatively long and the epipodials (radius, ulna/ tibia, fibula) are short – they are wider than long in some derived taxa (e.g. Dolichorhynchops). The mesopodials are disk-like and the metapodials and phalanges (finger bones) are elongate and waisted (pinched). Plesiosaurs evolved hyperphalangy (i.e. an increase in the number of finger bones), and often possess accessory bones in the epipodial/mesopodial areas (Figure 1.4). The flippers are curved posteriorly and taper to a sharp tip.

1.5 Taxonomic diversity
The colloquial term plesiosaur is a homonym. Strictly speaking the name is reserved for the order Plesiosauria but it is also popularly applied to the Plesiosauroidae, one of two superfamilies within the Plesiosauria sensu stricto (O’Keefe, 2001a). One should be cautious not to confuse these names with the family Plesiosauridae or the genus Plesiosaurus. According to the most recent published analyses of plesosaur systematics, there are several distinct plesosaur families distributed between the two superfamilies (O’Keefe, 2001a). The overall taxonomy proposed in this phylogenetic study closely mirrors traditional classifications (e.g. Brown, 1981). The following list represents a current taxonomic scheme for plesiosaurs with the colloquial terminology (as used in many popular accounts and throughout this Thesis) are given in brackets:
According to the analysis of O'Keefe (2001a), and as outlined above, the first major plesiosaur division is the superfamily Plesiosauroidea, which includes the families Plesiosauridae, Cryptoclididae, Elasmosauridae and the Polycotylidae (the last lineage is sometimes regarded as a pliosauroid family, based on its pliosauromorph morphotype). In spite of this phylogenetic work, the Plesiosauridae remains a poorly supported plesiomorphic group from the Lower Jurassic. As traditionally defined, elasmosaurids span throughout the Jurassic and Cretaceous (Brown, 1993; Grossman, 2007), while cryptoclidids also appear to have had a long distribution, ranging from the Middle Jurassic to the Late Cretaceous (Cruickshank and Fordyce, 2002); however, the taxonomic status of some of the later forms, sometimes included in the clade Cimoliasauridae (Persson, 1963; O'Keefe, 2001a), is disputed (Smith, in review). Certainly, based on the fossil record, polycotylids were the most recent plesiosaur family to diverge and are restricted to the Late Cretaceous. Their position within the Plesiosauroidea (rather than the Pliosauroidea with which they were traditionally allied) has been well demonstrated (Carpenter, 1996; O'keefe, 2001a), but has recently been challenged (Druckenmiller, 2006ab). These issues will be discussed in more detail based on the analyses presented in this thesis (Chapters 5, 6 and 7).

The second recognised plesiosaur superfamily is the Pliosauroidea and forms the focus of this thesis. The group is often colloquially termed 'pliosaurs' (e.g. Ellis, 2003) and includes at least two families, the Rhomaleosauridae and the Pliosauridae (O'Keefe, 2001a). Other authors recognise a further one, or two, families within this superfamily (Ellis, 2003), further differentiating some members, otherwise positioned in the Rhomaleosauridae, into a distinct family, the Leptocleididae (White, 1940;
Kuhn 1961, Persson, 1963; Druckenmiller, 2006), and/or differentiating some derived members otherwise positioned in the Pliosauridae, into a distinct family, the Brachaucheniiidae (e.g. Williston, 1925; Carpenter, 1996; Hampe, 1992, 2005). Presuming all four pliosauroid families are valid, the rhomaleosaurids and pliosaurids are restricted to the Jurassic Period; the leptocleidids and brachaucheniiids are restricted to the Cretaceous Period. Again, despite the phylogenetic work of O'Keefe (2001a) the rhomaleosaurids are poorly supported.

In summary, recent phylogenetic studies recognise four plesiosauroid families, Plesiosauridae, Cryptoclididae, Elasmosauridae and Polycotylidae. Four families of pliosauroid are recognised, Rhomaleosauridae, Leptocleididae, Pliosauridae and Brachaucheniiidae. This thesis is primarily concerned with the Rhomaleosauridae.

1.7 Thesis objectives
The main aim of this thesis is to assess the diversity and determine the phylogenetic position of *Rhomaleosaurus*. To achieve this, I present the first cladistic analysis of morphological characters dedicated to pliosaurs, and a morphometric analysis dedicated to Lower Jurassic pliosaurs. The broad objectives of this thesis can therefore be summarised as follows:

1. To fully describe all known specimens referred to *Rhomaleosaurus*;
2. To assess the anatomical diversity and revise the systematics of *Rhomaleosaurus*;
3. To determine the validity of the family Rhomaleosauridae;
4. To determine the interrelationships within the Rhomaleosauridae (if valid) and to determine the position of this clade within Pliosauridae and Plesiosauria

1.8 Thesis structure
In subsequent chapters, this thesis is structured to reflect the process through which contingent conclusions were drawn. Firstly, previous work founding the basis of this study is reviewed (Chapter 2 – Historical background). The specific history of each fossil specimen analysed during this project is then presented, along with a review of the basic palaeontological methods employed for illustrating the specimens (Chapter 3 – Material and palaeontological approaches). This is followed by an anatomical chapter, in which specimens are described and compared outside of any systematic framework (Chapter 4 – Specimen descriptions). A chapter of specimen-based
analyses is then presented (Chapter 5 – Morphometric and cladistic analyses) comprising a morphometric analysis and a cladistic analysis, the aims of which are to determine a sound systematic framework, a classification determining the taxonomic affinity of each specimen. This framework forms the basis for the subsequent chapter on systematic palaeontology, including revised diagnoses (Chapter 6 – Systematic palaeontology). Chapter 7 (Discussion) comprises a synthesis of all the results drawn from the thesis, and addresses the original aims outlined above. Finally, Chapter 8 (Conclusions) summarises the main conclusions of the thesis.