1 Introduction

The development of comparative anatomy has been neither progressive nor continuous. Progress has been halted by intellectual stagnation, by failure to capitalize on earlier discoveries and by religious and political intolerance. Rarely can major advances be attributed to individuals but are usually the outcome of centuries of human endeavour. The eight centuries of Greek objectivity were followed by a period of scientific and artistic stasis which lasted for more than a thousand years.

It is unclear as to whether the earliest studies of animal anatomy were based primarily on a desire to study animal structure *per se*, or because of a hope that light might be thrown on the morphology of man. Animal dissections by both zoologists and anatomists date at least from the time of Aristotle (*c.* 384 BC) and reveal an objectivity common with other facets of Greek culture. However, the foundations for much of this scientific thought were developed in the earlier civilizations of Babylon and Egypt and were then developed by Greek philosophers primarily to assist and explain human problems. Aristotle's contributions to both zoology and comparative anatomy were extensive and his *History of Animals, the Parts of Animals and the Generation of Animals* establish him beyond question as the founder of the biological sciences. Descriptions of the nictitating membrane of the eye, os cordis of the horse and ox and the os penis found in many carnivores were based upon his own dissections, although subsequent errors in translations of his works have seriously reduced our knowledge of the actual number of animals Aristotle studied. In common with other Greek scientists of his time, his work was based on observation but he founded the method of biological assessment which in essence is still in use today. First, statement of the problem, then discussion of previously published work before finally drawing conclusions. Even so, factual errors occur such as his belief that the wolf and lion have only one cervical vertebra. Although dividing the animal kingdom into the equivalent of Invertebrata and Vertebrata with recognition that Cetacea were not fishes, he made no direct attempt to draw up a comprehensive classification of species based on specific criteria, although his writings suggest that he was moving towards a *natural* classification. His wide ranging interests certainly provided much anatomical information, although it remains unclear as to how much was original and how much came from studies made by others. Despite his absorption with all aspects of human life, however, there is no record of his dissecting the human body, possibly reflecting the social and religious mores of the times.

Galen (*c.* AD 130–201) lived when Greek culture was in decline. His interests, in contradistinction to Aristotle, lay in the morphological and physiological aspects of biology. As an observer and experimentalist much of his writing is said to represent the anatomical traditions of his time and thus perpetuate many errors of fact, whilst at the same time perpetuating his pre-eminence in the field of biology for many centuries. He founded a system of physiology based upon experiments carried out on living animals, this included observations that in the living animal the left ventricle and arteries generally contain blood and not air, thus correcting a belief that had existed for over three hundred years. His demonstration that nerves originated in the brain and spinal cord rather than the heart was again a fundamental discovery; but these fundamental discoveries were combined with a mixture of established facts and misconceptions, many of which were to persist well into the twelfth century.

There is reliable evidence that Galen dissected a wide variety of animals including numerous mammals. Amongst these were both tailed and tailless primates and as was common at this time he transferred by analogy his conclusions to 'Man'. As physician to the gladiators in Pergamun, Galen must have been in an excellent position to observe much human anatomy, both internal and external, but recorded few of his conclusions (Cole, 1944).

With the death of Galen in AD 200 and the gradual decline in Greek culture and philosophy, the tradition of biological learning virtually ceased in Europe. Translations of texts into Latin in the eleventh and twelfth centuries resulted in blind acceptance of what was in essence, outdated dogma. For many centuries Mankind was to be either indifferent to the mysteries of Nature or attempt to penetrate them by a mixture of pious belief and literary research. The revival of learning, when it arrived, was due to the invention of movable type rather than any change in philosophical beliefs. Prior to this the diffusion of knowledge had been gradual and restricted to hand copied manuscripts usually compiled within monasteries, where the Abbot might be expected to be watchful for potential heresies! It is hardly surprising therefore that between the eclipse of classical learning and the invention of printing in the fifteenth century, anatomical research was largely in abeyance. Scientific research of all kinds was considered unnecessary, even forbidden, and Greek teachings were accepted as authoritative by University and Church.

Standing virtually alone during this barren period was the majestic figure of Leonardo da Vinci (1452–1519), whose interest in comparative anatomy was the result of his work as painter and sculptor. He combined the detailed objectivity of the anatomist with the vision and aesthetic sense of an artist and was greatly interested in the general structure of the human. When mystified despite having dissected more than 30 human bodies, he turned to comparative anatomy for solutions. Had his findings been published at the time they would surely have had a profound influence on biological thought. However, he was denounced by the Pope for the practice of human anatomy, his contemporaries bitterly opposed many of his discoveries, such as 'that the heart was a muscle', and his manuscripts only became widely available 200 years later. His techniques are still partially known and include the making of wax casts of the cerebral ventricles and the use of serial sections. He dissected many animals including primates and his descriptions of the facial muscles of the horse remain masterpieces of accuracy (Hopstock, 1921).

Prior to the development of movable metal-type, printing manuscript copies of documents was slow and laborious. The biological works of Aristotle were said to have been copied more extensively than those of any other scientist during these Dark Ages, yet few remain in existence. The first of the great biological works to be published during the sixteenth century was the *Fabrica* by Vesalius in 1543. Although possibly the 'Father' of modern anatomy he was not a comparative anatomist, being analytical and unimaginative rather than constructive in outlook. His contribution to progress was in establishing the anatomical method by which he showed that progress in science was possible only by research. Authority, no matter how firmly established, must give way to the findings of original investigation; by this dictum he generated implacable opposition. He accepted the authority of the human body as revealed by dissection, rather than relying on Galen's view which was derived largely from animal dissection. 'Galen', said Andreas Vesalius, 'imposed upon us the anatomy of the ape.' Even so Vesalius's debt to Galen was considerable, for the former's physiology is but a revised version of Galen's earlier experimental system. Apart from the illustrations, the *Fabrica* is based largely on Galen with its text Grecian in outlook. Factual errors that were said to have been imported from animal anatomy were thought to have been corrected, but many new ones were left uncorrected. Notwithstanding this, *Fabrica* remained the most important anatomical reference book of its day and its author the leader of the scientific revolution of the sixteenth century. Embittered by local opposition, Vesalius gave up scientific research to become personal physician to the Spanish monarchs Charles V and Philip II. He was accused of opening the chest of a supposedly dead nobleman only to find the heart beating! For this he was sent to Jerusalem as a penance, was shipwrecked on the return journey and died in 1564 on the Greek island of Zakinthis (Dunning, 1993).

The revival of research in comparative anatomy may be dated from the publication in 1551 by Pierre Belon on various '*Cetacea and other Marine animals*'. Although dissecting three species of cetaceans and noting many of their mammalian characteristics he related them to the fishes. Similarly bats were put amongst the nocturnal birds of prey. It was inevitable that such early studies in comparative anatomy would be deficient in morphological accuracy, for knowledge of descriptive anatomy was itself at a primitive stage forestalling significant comparisons. More important than Belon was Frisian Volcher Coiter whose works were published between 1572 and 1575 (Cole, 1944). A student of the Fallopian School of Padua he urged the comparison of human anatomy with that of beasts, and although well versed in human anatomy his prime interest lay in dissections of a wide variety of mammals, amphibians and aves. His researches into the growth of the skeleton in the human foetus showed that bones are preceded by cartilages and the importance of centres of ossification. Although his studies embraced a wide range of animals his main contribution to mammalian anatomy was based on studies of the skeletons of more than 50 species, including both tailed and tailless primates. The first comprehensive monograph devoted to a single species, the horse, was published in 1598 by Carlo Ruini (a senator of Bologna) one month before his murder. There is suspicion that the plates used in this monograph were those drawn by da Vinci for his own proposed treatise but prior to this publication the anatomy of the horse was largely unknown, despite it being such a well known domestic animal. This work was the logical outcome of the Vesalian tradition, topographical but logical in its schematic approach to the horse's system. It passed through 15 editions between 1598 and 1769 despite extensive plagiarism and prejudice. Dissection of such a large unpreserved animal must have presented many technical problems but was made possible by Ruini's knowledge of human anatomy. However, the absence of a comparative bias hindered the identification and naming of the musculature and he failed to recognize the absence of a clavicle.

Records of the anatomy school at Padua go back at least to 1387, although its most brilliant period was in the sixteenth and seventeenth centuries. During this time the famous Chair in Anatomy was occupied by Vesalius, Columbus, Fallopius and Fabricius. The latter, a convinced and ardent Aristotelian and

Galenist, attempted to combine scholasticism with research, although both approaches to furtherance of knowledge were mutually exclusive. Although primarily interested in comparative embryology he must be credited for being the first to investigate the physical importance of animal structure. In 1594 he built, at his own expense, the famous ‘Anatomy Theatre’ to accommodate his large classes and it was here that he first dissected publicly the human body.

Many of Fabricius’s publications on embryology and morphological anatomy compare the human with other animals, assessing differences and factors in common both in structure and function (e.g. Fabricius, 1600). Studies included the alimentary canal and later the compound stomach and physiology of rumination in animals such as the sheep, goat, ox and deer. Other comparative studies included the eye, respiratory system and ear. If the work of Fabricius lacked philosophical interest it undoubtedly exercised a considerable influence on the development of anatomical science. Vesalius had concentrated on human anatomy to the exclusion of comparative mammalian anatomy. Fabricius by stressing the importance of comparative studies restored interest in animal dissection influencing his successor Casserius who in 1600 promulgated his classic investigations on the organs of sense and voice (Casserius, 1601).

The anatomy of the vocal and respiratory tract

Preeminent amongst the earlier anatomists in his interest in the physiology of the nervous system was Galen. Although only recognizing seven of the cranial nerves he compared the recurrent laryngeal nerves in several species including ox, dog and bear. Sensory and motor nerves were distinguished by variations in texture but his investigations into the neurological control of muscles led to research into the production of voice by the larynx and the function of respiratory muscles. This interest in the larynx was continued by Leonardo da Vinci who examined various carnivore larynges recording his findings with commendable accuracy. Vesalius demonstrated that cutting the recurrent nerves ‘silenced the voice’ but was unable to dissect the brain because of ecclesiastical pressure. His experiments on the respiratory movements of the chest, lungs and diaphragm were performed on dogs and pigs, virtually his only interest in comparative anatomy. He had criticized Galen for introducing animal anatomy into his illustrations of human anatomy but the figure of the hyoid bone in his own treatise comes from the dog and the recurrent laryngeal nerve is not human.

Belon (1551) discovered the function of the intranarial epiglottis in cetaceans, understanding that despite an aquatic life they were transnasal air breathers. However, the most detailed account of mammalian laryngeal anatomy is by Ruini (1598) in his classic description of the horse. Cartilages, muscles and epiglottic function are all accurately recorded as is the course of the recurrent laryngeal nerves, although the latter are erroneously thought to be branches of the spinal nerves. In 1600 Fabricius wrote full accounts of the comparative anatomy of the laryngeal region of several mammals including the ape but tried to homologize the laryngeal cartilages of birds and mammals (Figure 1.1). Later he entered the difficult field of phonetics discussing the physiology of voice production, functions of laryngeal structures and the possible reasons for the anatomical placement of the larynx. The speech of humans is compared with animal vocalization using air blown through an excised larynx to illustrate the importance of the vocal cords in sound production. Considering his poor reputation as a comparative anatomist these investigations were of considerable importance, providing considerable stimulus to his successor Guiulio Casserius. Despite his humble background (Casserius was man-servant to Fabricius) his publications on the sense and voice organs (Casserius, 1601) represented the most ambitious and detailed investigations on comparative anatomy carried out at this time. Although limited in scope, his dissections illustrated the anatomy of the larynx and chest in the human, ape and more than 20 other mammals. The recurrent laryngeal nerves were now correctly assigned to the sixth pair of cranial nerves and their pathway around the subclavian on the right and aorta on the left correctly described. The larynx was recognized as the principal organ of voice production, the cartilages and intrinsic muscles clearly identified. A long philosophical discussion on the definition, nature and cause of voice was unaccompanied by any experimental evidence although the larynx is identified as the source of sound rather than the movement of the lungs. Extension of this interest in sound production to the invertebrates provided the first account of the timbale found on the abdomen of the cicada and he was aware that in some crickets stridulation is produced by friction of areas on wing surfaces.

William Harvey (1578–1657)

Early anatomists were preoccupied with human anatomy despite the difficulties and perils attached to human dissection. Cadavers were difficult to obtain and the study of human anatomy was viewed by an unenlightened public with disgust and by the Church as anti-religion. In the seventeenth century the emphasis on experimentation and measurement with increasing conviction that the body

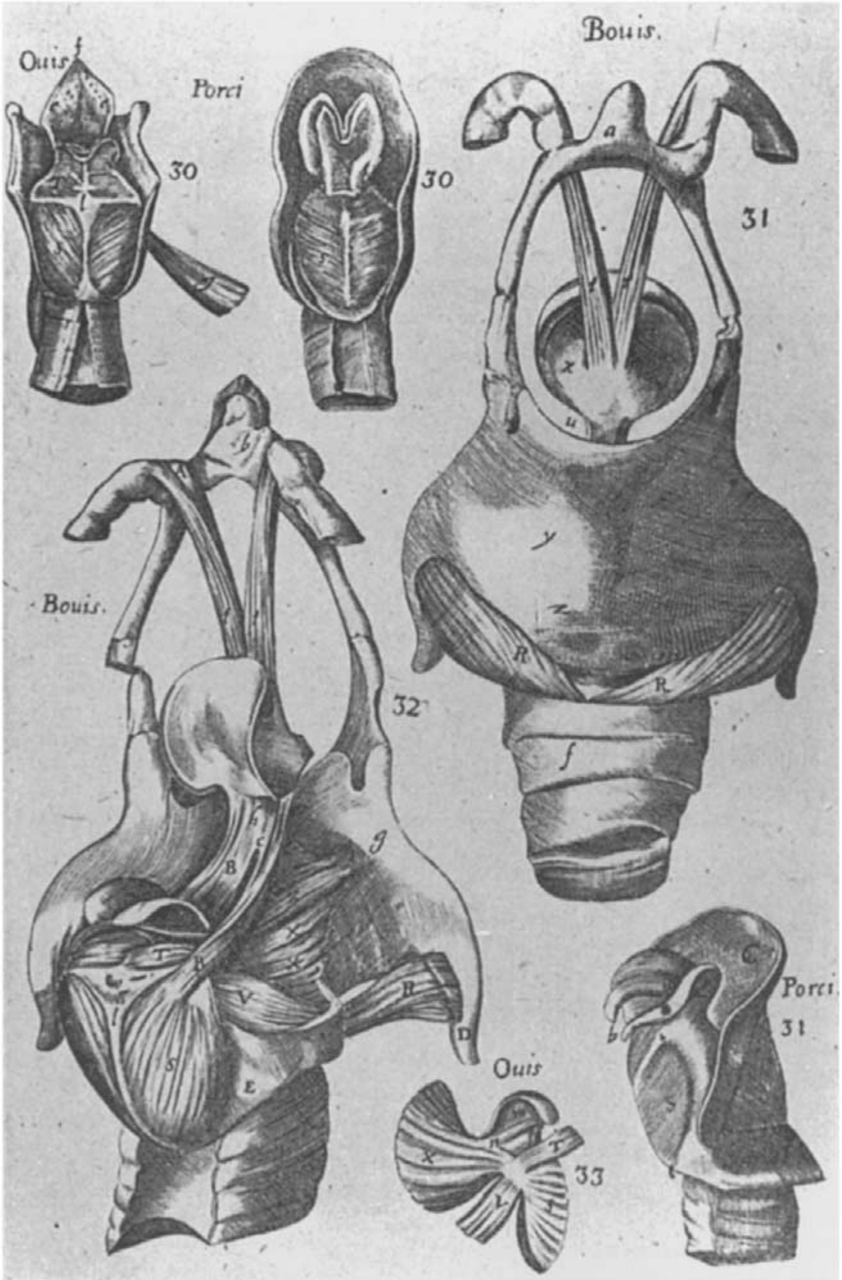

Figure 1.1. Larynges of pig, ox and sheep. (After Fabricius, *c*. 1600.)

could be understood by mechanical principles, were expressed through a preoccupation with bodily mechanisms. The embryological explanation for the variations in routing of the recurrent laryngeal nerves was still unknown and William Harvey developed a mechanistic theory of voice production based on supposed similarities with cords stretched around pulleys. Although visualizing the need for research, he remained misled by the tyranny of the Greek tradition and engaged in a long philosophical exposition on the nature and causes of voice production without carrying out any experiments to support his suppositions. Nevertheless the prophetic genius of Harvey saw the real value of research in non-human mammals in that it overcame the inherent difficulties of investigating the relationships between structure and function in humans. He applied this method most successfully to his studies on the function of the mammalian heart (Harvey, 1628).

Anatomy began to progress again, just as it had following publication of the *Fabrica* of Vesalius and by the end of the seventeenth century a considerable body of reliable information within the biological sciences had been established. Marco Severino, a close contemporary of Harvey, published his treatise *Zotomia Democritaea* in 1645. When comparing the anatomy of the human and the ape he was so impressed by the obvious affinity that he recommended that the ape should be used for all medical research, although as an anatomist he preferred the pig! His advocacy for repeated and varied animal dissections was based on the premise that 'structures might be well developed in one species but absent or less developed in another'. However, in common with most other comparative anatomist-surgeons, identification of the more unusual species that he described remains in doubt and his publications consist largely of brief accounts of often unrelated and sometimes inaccurate anatomical facts.

The new age of comparative anatomy

Acceptance that progress could only be made by combining research with accurately observed morphological information, led to the accumulation of considerable amounts of new and reliable data. In time this formed the basis for a system of comparative anatomy whose foundation had been laid by Ruini at the end of the sixteenth century (Cole, 1944). The most distinguished members of this monographic school of animal anatomy now included Malpighi, Tyson and Swammerdan who in their concern for anatomical investigation rather than philosophical discourse filled the transition period between William Harvey (1578–1657) and John Hunter (1728–93). Malpighi was born in 1628, the year which saw the publication of Harvey's work on the circulation. In 1661 Malpighi demonstrated the true nature of the lungs and with the discovery of the blood capillaries, laid the foundation of our knowledge of the physiology of respiration. His most important publications are thought to have been devoted to the structure and life history of *Bombyx mori*, a silk-moth. Tyson however, was primarily interested in the respiratory system of the Cetacea describing the special adaptions of their larynx necessary for an aquatic but air-breathing existence (Tyson, 1680). He concluded 'that it was somewhat inserted into the bottom of the nasal passage and that it was different from other animals', and observed that the blow-hole corresponded to the nostrils of other animals. This was based on studies of the porpoise and supplemented the findings of others, for the Cetacea appear to have attracted considerable interest for more than a century (Belon, 1551).

Although Tyson studied a wide variety of unusual mammals, such as the peccary, noting the dorsal scent gland, its compound stomach and absent gall bladder, he also gave the first account of the anatomy of a marsupial, the opossum. Besides these valuable contributions to comparative anatomy his most important publication was a monograph on a young 'Pigmie', which he proved was not an undeveloped human or monkey (Tyson, 1699). At this time the anatomy of the higher anthropoids was unknown, even the appearance of these animals was familiar only to a few explorers whose accounts attracted general disbelief. The gorilla was first discovered in 1847 and although the orang-utan had been described in 1658 its anatomy was not detailed until 1778, when Pieter Camper identified it as Tyson's 'Pigmie' (Camper, 1778). The chimpanzee 'emerged' in 1625 and was examined, though not dissected, by Tulip who, despite Rembrandt's celebrated 'Anatomy lesson of Dr Nicolaas Tulip' painted in 1632, was a local politician and successful physician rather than a comparative anatomist (Dunning, 1993).

Tyson must be credited for initiating studies into these human-like apes thus recognizing the existence of a new species of primate intermediate between humans and monkeys. His problem was to determine the status of these higher anthropoids and following a decision that the ape was indeed a true species, compiled a list of their most significant anatomical features. From this it was possible to assemble groups of characters which served to emphasize an affinity between different species, a system not entirely dissimilar from that used today by zoologists. Despite his dominant role in seventeenth-century medicine and the volume of animals dissected during his research on the brain, Thomas Willis made little contribution to our knowledge of mammalian comparative anatomy. What little was recorded in his *Soul of Brutes* (1672) appeared to be surplus to his arguments which themselves bore a close relationship to the more pedantic forms of classical Hellenist philosophy. However, this was the period during which Dutch science was paramount throughout Europe and it was their scientists who were to make great contributions to the progress of comparative anatomy. Foremost was the amateur Antony van Leeuwenhoek (1632–1723), who despite an unrestrained desire to place his preliminary and often undigested thoughts in print, must be credited as the originator of microdissection as an essential tool of anatomical research. A notable feature of his work was that having made an important observation in one animal he would then search for a similar feature in other species, despite his belief in the fixity of species. His manipulative skill must have been astonishing, for although it is recorded that he used more than 400 microscopes which magnified up to 200 diameters, the lens was single and biconvex. Although not considered an originator of many comparative anatomical discoveries, he was particularly interested in aphids and gnats, his microscopical approach was revolutionary in his day setting the scene for those who would follow. Jan Swammerdam, the son of a prosperous apothecary in Amsterdam, was in contradistinction trained in science. Born five years after Leeuwenhoek, he spent much of his early years unprofitably cataloguing the family museum before commencing his most important work on respiration which was published as his Doctorate dissertation in 1667. This became one of the classics in the history of physiology, describing experimentally the mechanism of mammalian respiration. However, most of his publications relate to Invertebrata, again using the microscope. Sadly he drifted towards the unrewarding distractions of mysticism and spiritual exaltation, dying it is said ‘in the turmoils of an unbalanced mind convinced that the pursuit of natural knowledge was vain and impious’. Yet his work on respiration and the treatises on insects remain a monument to his genius.

Learned societies and institutions

The addition of research to the simple collection of scientific facts eventually resulted in a degree of co-operation between individuals with similar interests and of like mind. In London this may well have been the intention of Boyle’s ‘Invisible College’, which in 1660 became the Royal Society. The main objective of this learned society was the ‘advancement of experimental learning by organized research’, although at the same time members were reminded to remain aware of the decorum expected of their scientific profession (Birch, 1766). From its foundation, members showed great interest in anatomical studies although it appears from the *Royal Society Transactions* this interest was primarily medical rather than purely biological. Early volumes included descrip-