1a) Describe the phylogenetic and ontogenetic origin of the axial skeleton.

**Ontogenetic origin:** The axial skeleton forms from mesodermal cells from the sclerotome of the epimere. Early during development, the mesoderm begins to differentiate into three parts, the epimere, mesomere and hypomere. The epimere is the most dorsal portion of the differentiating mesoderm and it subsequently differentiates into three parts, the sclerotome, myotome and dermatome. The sclerotome forms from the dorso-medial surface of the epimere and migrates in towards the notochord and subsequently condenses to form the axial skeleton. *(10 marks)*

**Phylogenetic origin:** The original function of the vertebral column was to protect the spinal cord and dorsal aorta. The structural support for the longitudinal axis of the body came from the notochord. The elements of the vertebral column first appear as small cartilaginous elements resting dorsally upon the notochord in lampreys. The first components of the vertebrae to appear were the dorsal and ventral arches that rested on the notochord. Subsequently, the dorsal arches, and the neural and interneural elements (intercalary) appear to protect the neural tube while ventral, hemal and interhemal arches protect the blood vessels. The notocord still provides support. *(5 marks)*

The next step in the evolution of the basic elements of the vertebra was the formation of two centra, the intercentrum and the pleurocentrum. These formed from the expansion of the ventral arches where they met the notochord. This was the situation in primitive chondrichthyans but in extant sharks, these vertebral elements enlarge to become the predominant structural element of the body axis. The notochord remains but is constricted and enclosed within the vertebral centra. In advanced fishes, the vertebral column is ossified and the centra become more prominent and replace the notochord as the major structural support for the body. Neural spines and ribs become more prominent. *(5 marks)*

The trend is to then reduce the contribution from the notochord while leaving intervertebral bodies (cartilage) or intervertebral disks (mammals) between the vertebrae. Thus, the centrum gradually replaces the notochord within the vertebrae while the notochord becomes confined to the concavities at the articular ends of the centra and are usually capped with cartilaginous pads. *(5 marks)*
1b) Describe its form and function in each major vertebrate group

The form and function of the vertebral column are related directly to the static and dynamic demands placed on it. Static demands are associated with suspension or weight bearing. Dynamic demands are associated with locomotion. These are related to the environment the animal is in - aquatic or terrestrial - and the type of locomotion in which the vertebral column is involved. (5 marks)

Agnathans have a large and prominent notochord. Vertebral elements are absent in hagfish and are small cartilaginous elements resting dorsally upon the notochord in lampreys. The notochord is the major source of support. In sharks there is a cartilaginous vertebral column surrounding the notochord. The vertebral elements are the main structural elements. (5 marks)

In Chondryichthyes and Osteichthyes, support is provided by the water. The vertebral column serves primarily as a "compression girder resisting telescoping of the body during locomotion and translating axial muscle forces into lateral swimming undulations". This means that the vertebral column is flexible enough to bend a little, becoming compressed on the bent side. If it couldn't compress, it couldn't bend. It is also stiff enough to resist collapse or buckling or folding. It doesn't compress too much. Thus alternating contractions of muscles on each side of the body produce lateral undulations that provide the propulsive force to push fish forward through the water. (5 marks)

The same lateral undulations of fishes are important for the locomotion of the early tetrapods. Now, however, besides bending from side to side due to locomotion, the column tends to bend dorso-ventrally due to the weight of the animal hanging from it suspended between the limbs, as well as the weight of the head at the front end. Thus the tetrapod vertebral column incorporates design features to deal with this. The vertebral column must be both strong for support – yet have some flexibility for movement. The trend is to reduce the contribution from the notochord while leaving intervertebral bodies (cartilage) or intervertebral disks (mammals) between the vertebrae. Intervertebral ligaments control the stiffness of the vertebral column when it does flex. Torque also becomes a problem in tetrapods and anti-torque features appear in the design of the column in the form of the zygapophyses. (5 marks)

With this trend, vertebrae take over the role of axial support and become important attachment sites for body musculature. As such, the axial skeleton becomes critically important for transferring muscle contraction into body movement for locomotion. In tetrapods, the role expands to include suspension of the body. (5 marks)
1c) Discuss how form and function of the axial skeleton have evolved to allow different vertebrate groups to exploit different environments and lifestyles.

**Fluid Environment**

For aquatic organisms, the endoskeleton does not play much of a role in support. Most animals are close to being neutrally buoyant and their weight is supported by the water around them. We do not see many adaptations to the axial skeleton in this group. (5 marks)

**Terrestrial Environment**

The transition from water to land was accompanied by the mechanical demands placed on the axial skeleton. For terrestrial animals, gravity becomes a problem. They must either rest fully on the ground or be supported by legs. (5 marks)

**Bridging**

*Forces acting on pillars:* When a material bends under a load, compressive forces develop along the concave side and tensile forces along the convex side. When the supportive column is loaded symmetrically, the only type of force experienced is compressive force. Asymmetrical loading of the same mass causes a column to bend. The column experiences compressive forces and tensile forces which are greater near the surface and diminish towards the center of the column.

*Forces acting on the spinal column:* Since the weight of the viscera, hangs from the vertebral column between the two pair of legs, the load will tend to compress the bones on one side of the legs and stretch the bones on the other side (put them under tension). These compressive and tensile forces can be offset if equal, and opposite forces are applied from the other direction. This is a form of cantilevering. In the case of tetrapods, the tail acts as a cantilever at one end and the head at the other. (10 marks)

The vertebral column itself will have forces acting to cause it to bend, placing the column under compression on the bottom. The ligaments that join the vertebrae together will oppose this tendency by being placed under tension. As long as the forces are equal and opposite, the structure is solid and stable. (5 marks)

**Design of Vertebrae**

*Angle of the Neural Spines:* The angle that the neural spine makes with its centrum usually reflects the forces being placed upon it. The tensile ligaments, and the axial muscles attach to the spines and exert forces on them. Muscles will attach from both the front and the back. The resultant force placed upon the spine will be the net sum of these forces acting from both directions. The spines are strongest when the net sum produces a force that acts along the spine towards the centrum (it is under compression). Also, bones tend to grow as a result of the forces placed on them. The net result is that the direction of the spine reflects the direction of the resultant force imposed upon it by all axial muscles inserted on it. (5 marks)
Height of Neural Spine: The height of the neural spine is proportional to the mechanical leverage the muscles must exert to move or stabilize the spinal column. To counter increasing forces acting on a neural spine, you could either use larger and larger muscles, or use a longer lever (or both). Vertebral designs incorporate modifications to meet mechanical problems. In many animals the height and direction of the spines within the same vertebral column indicate the specialized functions served by different sections of the vertebral column. (5 marks)

Regionalization of the Vertebral Column: In fishes the vertebral column is differentiated into two regions, the trunk and the tail. The centra are undifferentiated reflecting the fact that the column is not used for support. The only differentiation is whether the vertebrae receive ribs or hemal arches. (5 marks)

In tetrapods, the column supports the body and receives and transmits the forces from the limbs that generate locomotion. Since diverse forces are placed on different parts of the column, not surprisingly we see differentiation of specialized regions. The first two regions to specialize in early vertebrates are the sacral region for the attachment of the pelvic girdle and the hindlimbs, and the cervical region allowing some freedom for the head to turn independently of the body. (5 marks)

The trunk region subsequently differentiates into the thoracolumbar region which ultimately becomes the thorax and lumbar regions. The thorax has ribs and the lumbar region does not. The origin of a separate, ribless lumbar region is believed to reflect increasing speed of locomotion on land. The presacral region is the region that experiences the greatest lateral flexion during terrestrial locomotion in quadrupeds and it is thought that the ribs interfered with rapid movement and thus they were subsequently lost. (5 marks)