I. INTRODUCTION

The fossil evidence of the earliest known vertebrates is rather fragmentary. The knowledge of the first known vertebrates comes from the bony scales deposited in the Ordovician fresh-water sediments (Moore-1949 & Colbert-1955). They are believed to be the scales of agnathous vertebrates popularly known as Ostracoderms and it is generally agreed that Ostracoderms originated in Ordovician times (Simpson-1952, Romer-1953 etc.). Complete, adequate and identifiable deposits are however obtained in the late Silurian deposits. It was the time when jawless vertebrates were succeeded by the primitive gnathostomes viz. Placoderms. They were found for the first time from the fresh-water deposits of the late Silurian period (Romer-1953). The appearance of the jaws gave immense advantage to these vertebrates. To quote Colbert (1955), "It opened to the vertebrates new lines of adaptations and new possibilities for evolutionary advancement". Besides the possession of jaws, it seems quite likely that at least some Placoderms were in the possession of functional lungs. Impressions of the portions of the soft parts preserved in Bothriolepis, one of the placoderms of the upper Devonian, indicates that this vertebrate was already in possession of well developed and probably very functional lungs (Colbert-1955). This view has also been supported by Watson (1926) and Romer (1949 & 1953).

There is a concensus of opinion that the Placoderms gave rise to early bony fishes, though is not very clear as to which group of Placoderms, the ancestors of these fishes belonged. The earliest known fossils of these fishes appear in the fresh-water deposits of Middle Devonian age (Colbert-1955). If the early teleostean fishes arose from these early bony fishes, it is evident that their marine representatives must have formed an off-shoot from their fresh-water ancestors. Such a view has been propounded by Homer Smith (1932 & 1953) on the bases of his findings on the nature of the kidneys in marine teleosts. Baldwin (1949), Romer (1946 & 1955) and others are also agreeable to this view. Another off-shoot of these early bony fishes gave rise to the Crossopterygians, popularly known as lobe-finned fishes. One of the earliest and the most primitive members of this group seem to be Osteolepids which are found for the first time from the middle Devonian deposits. An Osteolepid fish shares with paleoniscids - the primitive actinopterygians - and early Dipnoi, certain common features. Osteolepids are believed to be the probable ancestors of the first land vertebrates, viz. the primitive amphibians (Young-1951).

The definite advantages of a land life to the early amphibians is a matter of speculation. Romer (1953) suggests that in times of drought, it enabled these animals to change their dried aquatic habitats for better ones. It is well known that during the late Devonian period, when the advanced air-breathing bony-fishes became transformed into primitive

amphibians, droughts were prevalent. Under these circumstances, an excursion could be conducted by the primitive amphibians in an effort to reach water which was so essential for these animals to live. This suggestion of Romer seems to be quite logical. Possibly there were also other gradual series of changes taking place through time during this period and that the new adaptation could be used with advantage.

Speculating from the fossil records, the history of vertebrates during the Silurian and Devonian period seems to be a history of the animals which inhabited fresh-water. It is therefore suggested that "the shallow waters of continental drainage systems were the environments in which the primitive pre-Devonian vertebrates enjoyed their evolutionary success" (Colbert-1955), though it is generally agreed that the invertebrate progenitors of these animals were inhabitants of the salt-water (Young-1951, Romer-1953 etc.).

One of the early achievements of the vertebrates during this period as has been mentioned earlier, were the formation of the jaws and possibly the development of the lungs for breathing atmospheric air. As to the latter habit, it is not clear as to when it was achieved. The modern authorities including Watson (1926), Romer (1946, 1949 etc.), are of the opinion that the primitive bony-fishes were already in the possession of typical lungs. This habit was no doubt prevalent among the choanate fishes of the Devonian viz. crossopterygians and dipnoans. It is also quite likely that this habit was also

prevalent among the Devonian Actinopterygii. It appears that the Devonian Actinopterygii, viz. Paleoniscid fishes, possessed an air-bladder having a wide opening leading to the pharynx and that they breathed air (Young-1951). Polypterus, a modern descendant of the Devonian paleoniscids, which lives in African waters of to-day, has a similar arrangement. The subsequent evolutionary history of the actinopterygians indicates that this lung was being gradually transformed into air-bladder. While chondrosteans possibly retained lungs for air-breathing, in Holostei, it was almost transformed into air-bladder. The living Holostei of to-day, the Amia, possesses a single dorsal air-bladder, which functions slightly as a lung in the living forms, although its chief function is hydrostatic (Romer-1953). In the living Teleostei however it is not generally used for breathing purposes. In most of the cases, it serves as a hydrostatic organ.

The lungs seem obviously to be of a great advantage to the piscine fauna of the Devonian, which is well known for its seasonal droughts (Gregory & Barret — 1931). With the approach of settled conditions of the late Devonian and the period that followed thereafter, lungs were perhaps no more necessary. It is therefore reasonable to believe that either this lung disappeared gradually, or else it was switched on to some other use. In most of the cases the lung was converted into the air-bladder which serves the purpose of a hydrostatic organ. Similar views to the effect that the air-bladder of modern

Actinopterygii may have been derived from the lungs has been expressed by several authors including Goodrich (1930), Norman (1947), Young (1951), Simpson (1952), Smith (1953), Colbert (1955) and many others. The history of the evolution of the early vertebrates thus indicates that the air-breathing habit among the fishes was adopted at an early period. Nor was this habit restricted to choanate fishes. In all probability the Devonian Actinopterygii also had functional lungs. Whenever this habit might have come about among the Actinopterygii, a number of teleosts of to-day inhabiting both fresh-water and marine habitats have taken to air-breathing habit. Moreover to-day this habit is not restricted to Osteichthys alone. A few cases of air-breathing fishes have been noted among Indian elasmobranchs also. A feature common to all these fishes is that, they are the fishes living in waters adjoining land or similar habitats.

The air-breathing habit among the teleosts attracted the attention of workers as early as the beginning of the nineteenth century. In India, not much was known about these fishes until the beginning of the latter half of the nineteenth century. The earliest record in this matter is that of Day (1868), who made a mention of the fact that some of the fresh-water teleosts obtained air directly from the atmosphere. He also conducted experiments on Ophiocephalids, as a result of which he divided the Indian teleosts into two categories viz. (i) the water-breathing fishes, which use oxygen dissolved in water for

breathing purposes and (ii) the air-breathing fishes which in addition to making use of oxygen dissolved in water in breathing, also came to the top to breathe atmospheric air. Another publication which was made soon after, was that of Dobson (1874), who wrote on the amphibious nature of fishes of India. Day published another paper in 1878 pertaining to air-breathing habit in fishes. The monumental work of Day, published in two volumes entitled "The fauna of British India - Fishes" in 1889, gives an account of the habitat, structural adaptation in regard to air-breathing and the morphological description of aerial respiratory organs in a number of Indian teleosts.

During the present century numerous workers in India have made valuable contributions towards this subject. Regan as early as 1909 and 1911 published two papers on air-breathing fishes belonging to the family Anabantidae and symbranchoid eels. During the last 30 years a number of valuable and interesting papers have been published by Das & Hora. Das has published several papers since 1927 on various aspects of air-breathing fishes including the bionomics of the air-breathing forms, the development and structure of the air-breathing organs etc., of a number of air-breathing teleosts such as the climbing perch, Anabas (1928), the symbranchoid eel, Amphipnous cuchia (1929 & 1946), Gobiids including the mudskipper Periopthalmus (1930, 1932, 1938 & 1940), and Pseudapocryptes lanceolatus (1933 & 1934) and a loach, Lepidocephalus guntea (1935, 1936 & 1937). He has

also conducted asphyxiation experiments which show that air-breathing is essential to these forms (1927, 1928, 1938, 1940 etc.). He has further dealt with all these aspects and has also discussed in his presidential address before the Indian Science Congress in 1940, the probable causes which induced the development of the accessory respiratory organs in those forms. The work of Hora includes a study relating to the air-breathing mechanism and the physiology of respiration in a number of air-breathing teleosts (1932, 1933, 1935, 1939, 1941 etc.) and asphyxiation experiments conducted to find out the relative value of the aquatic and aerial breathing in certain forms (1935). He has also expressed his views on the probable causes relating to the development of air-breathing habit among the fishes (1935, 1939 etc.). Lele (1932), Ghosh (1933-34), Rao (1939) are also among those who conducted investigations on similar problems during this period. Recently in 1951 Menon has published a paper on the distribution of Clariid fishes. During the same year Krishnan Nayar has given an account of air-breathing in an estuarine eel, Amphipnous fossorius. George in his publication in 1953 has referred to air-breathing habit in two species of elasmobranchs viz. Chilloscyllium griseum and C. indicum. (Incidentally it may be mentioned here that air-breathing habit has been observed by me in another elasmobranch viz. Aetomyleus maculatus.) Among other recent publications include those of Mathur (1953) and Kulkarni & Jaggi (1954) on the air-breathing mechanism in some Indian teleosts viz. Rita rita and Megalops cyprinoides respectively.

Numerous papers on the bionomics, the air-breathing habit, structures of the various types of accessory respiratory organs, physiological aspects relating to this habit in fishes have been published in other countries too. Notable contributions of the investigators, those during the present century are Carter & Beadle (1930 & 1931), Carter (1931, 1935 & 1951), Breder (1931, 1941 & 1942), Schöötle (1931 & 1932), Bader (1937), Marlier (1938), Schlaifer & Breder (1941), Atz (1952_a, 1952_b etc.) and many others. The contributions made by Carter & Beadle are of special interest. Their work has been often referred to by various workers in the field both in India and abroad. Their careful investigations which include a study of the environmental conditions of the swamps of Paraguayan Chaco, the piscine inhabitants of these swamps and a description of the aerial respiratory organs in fishes such as Erythrinus, Hypopomus, Callichthys etc., have led to a better understanding of the subject.

A survey of the literature on the air-breathing habit in teleosts reveals that they can be grouped into various categories based on the nature of their aerial respiratory mechanism. Now it is known for instance that some teleosts utilize the organs associated with aquatic respiration viz. the gills, the buccal cavity and the branchial chambers for breathing atmospheric air. Then there are also fishes which have adapted organs which are primarily other than those associated with aquatic respiration (e.g. skin and intestine). Further, a few

forms have developed accessory respiratory organs in association with the gills, the buccal cavity and/or the branchial chambers with the help of which they draw atmospheric air for breathing. Taking into consideration these facts, one could easily surmise that the air-breathing habit among the progenitors of the modern air-breathing teleosts must have taken place in a number of directions viz. (i) by the retention of the air-breathing organs i.e. the lungs of the early bony fishes, (ii) by utilizing aquatic respiratory organs (i.e. gills) for breathing atmospheric air in addition to water-breathing as found in Hypopomus brevirostris, Haplochilus lineatus, etc., (iii) by adapting organs such as the skin and intestine which have nothing to do normally with aquatic respiration, (iv) by the development of the accessory respiratory structures in association with the organs of aquatic respiration and (v) the acquisition of the combined cutaneous and pulmonary respiration in addition to gill-breathing as prevalent among the immediate ancestors of the amphibia. This surmise is based on the fact that the first four lines are met with in modern fishes while, air-breathing as stated in the fifth occurs to-day in amphibians. While a majority of the descendants of these forms live in fresh-water, some forms are found to live in marine habitats also. One feature common to all these habitats is their vicinity towards the land. The present investigations concern mostly those which fall under the categories ii, iii and iv, to which most of the Indian air-breathing fishes belong. By way of comparison a relevant study has been conducted on some water-breathing teleosts also.

As regards the origin of the air-breathing habit among the fishes various explanations have been offered by several investigators. One however is impressed by the general belief that the lack of oxygen in the waters in which the ancestors of the modern air-breathing fishes lived has been a causative factor in the formation of the air-breathing habit. Carter & Beadle for instance state that "the aerial respiration in fishes has been primarily an adaptation to life in a medium poor in oxygen" (1931). As regards the air-breathing piscine fauna found to-day in waters rich in oxygen, one of these authors, Beadle states elsewhere (1933) that the habitats of the air-breathing central African fish found in well oxygenated waters are in open communication with swamps. He further states that at any rate before the formation of the rift valleys 'closed swamps' such as now exist in central South America were more general. Under such conditions he believes that the aerial respiratory organs of central African fish, which are now found in well oxygenated waters would have been of survival value. As regards the evolution of the air-breathing habit of fishes living in pools, marshes etc. known for less quantity of oxygen in their waters, Hora (1935) is quite in agreement with the views expressed by Carter & Beadle. As for the fishes living in waters rich in oxygen, he has offered alternate suggestions. He believes that the tidal influence is the probable cause which has induced the development of air-breathing fauna of the estuaries and sea-shores. As to the formation of this habit in the piscine hill-stream fauna he states that, "the fishes, with reduced gills which is

an adaptation to the torrential conditions of such waters, when compelled to live in overpopulated poorly oxygenated pools formed as a result of the breaking of the streams, are forced to breathe atmospheric air, as the undersized gills under the changed conditions are unable to draw all the oxygen requirements of these animals".

Whatever might have been the cause for the origin of the aerial respiration among the fishes, it is evident from the literature available that the piscine inhabitants of to-day are not confined to medium poor in oxygen. While this fact does not at all rule out the possibility of the progenitors of these fishes having taken to air-breathing in waters deficient in oxygen, the existence of the water-breathing forms in such waters raises some doubt on the accuracy of this statement. It was thought therefore advisable to study some aspects of air-breathing fishes with reference to Indian teleosts such as the probable evolutionary trends of the aerial respiratory organs, the external environmental conditions of the piscine habitats, the internal adaptations which make air-breathing a successful operation, the modifications brought about if any, in the associated structures (viz. the muscles), responsible for inspiration and expiration, the adaptational features of the aquatic respiratory organs (i.e. the gills) etc. and see whether such a work would throw any light on the origin and the evolution of the air-breathing habit among them.

The problem as thus envisaged comprises the undermentioned

investigations :-

1. The nature of the air-breathing organs met with among Indian air-breathing teleosts.
2. The disposition of muscles associated with respiration in certain teleosts.
3. The oxygen content of the media and a survey of teleostean fauna of the habitats inhabited by the air-breathing teleosts.
4. A comparative study of the oxygen-carrying capacity of the blood of water- and air-breathing teleosts.
5. The adaptational features in the gills of air-breathing teleosts.
6. The extent of gill-surface available for gaseous exchange in certain Indian teleosts.
7. The oxygen-consuming capacity of the gill-tissue of certain Indian teleosts.