Introduction[1]

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At a symposium on the biology of the southern cold temperate zone, held in London in December 1959 (Pantin, 1960), the senior author met Professor Paul Deraniyagala, Director of the National Museums of Ceylon who invited us to work for some time in Ceylon, under the Zoological Survey of Ceylon. The Survey was established with the support of the Government of Ceylon and UNESCO. The Director of the National Museums served as chairman. The main aim of the survey was to investigate areas under exploitation and those where exploitation was planned as a result of the rapidly increasing population pressure.

We found the invitation attractive and started planning an investigation of the changes in the physical environment, composition of the fauna and production in destroyed primary and re-established (secondary) ecosystems. The investigation was supported by King Gustaf VI Adolf of Sweden, the Government of Ceylon, the Swedish Academy of Science, the Swedish National Science Research Council, the Royal Physiographic Society of Lund, the National Museums of Ceylon, Magnus Bergvalls Stiftelse – Stockholm, and the Swedish Companies Svenska Ostasiatiska Kompaniet, Astra, Hässle and Leo.

Details of the field work are given below (p. XVI).

As a basis for specialists working on the material collected and as a background for field data and discussions of results, we consider it useful to give some information about the natural environments and resources of the island and their development. A few maps have been compiled, illustrating these conditions.

1. Morphology and geology

Ceylon is a detached part of the continental Dekkan plateau of ancient crystalline rocks. The interior of the island is occupied by the Central Highlands, a complex of plateaus, mountain chains, massifs and basins, at a general elevation of 1400 to 1800 m (Fig. 5). The highland is surrounded by two peneplains, the lowest of which (the lowland) extends from the coast inland where it rises to 100–150 m above sea level. The second peneplain (the upland) rises from this edge as an escarpment of about 300 m, at some places irregular and heavily eroded. The general elevation of the upland peneplain is about 500–700 m.

The highland may be divided into three portions, viz. the Knuckles Group to the north, the Central Massifs and the Sabaragamuwa Ridges to the southwest.

The highland and the upland are composed of crystalline Precambrian rocks, while much of the lowland is occupied by rocks of the Vijayan series of very strongly metamorphic palaeozoic rocks (Fig. 6).

Other geological formations occupy small parts of the island. Within the Vijayan series in western Ceylon there are two basins (Tabbowa and Andigama) of sedimentary rocks of Upper Jurassic age which form part of the Gondwana system. Tertiary rocks of Lower Miocene age occur as a thick belt of limestone in the northwest (Jaffna Limestone) and as a small outcrop at the south coast at Minihagalkande. Along the coast and in river valleys in many parts of the island there are Quaternary deposits of varying age and nature.

A full treatment of the geology of Ceylon

[1] Report No. 1 from the Lund University Ceylon Expedition in 1962 (Per Brinck, Hugo Andersson, Lennart Cederholm).

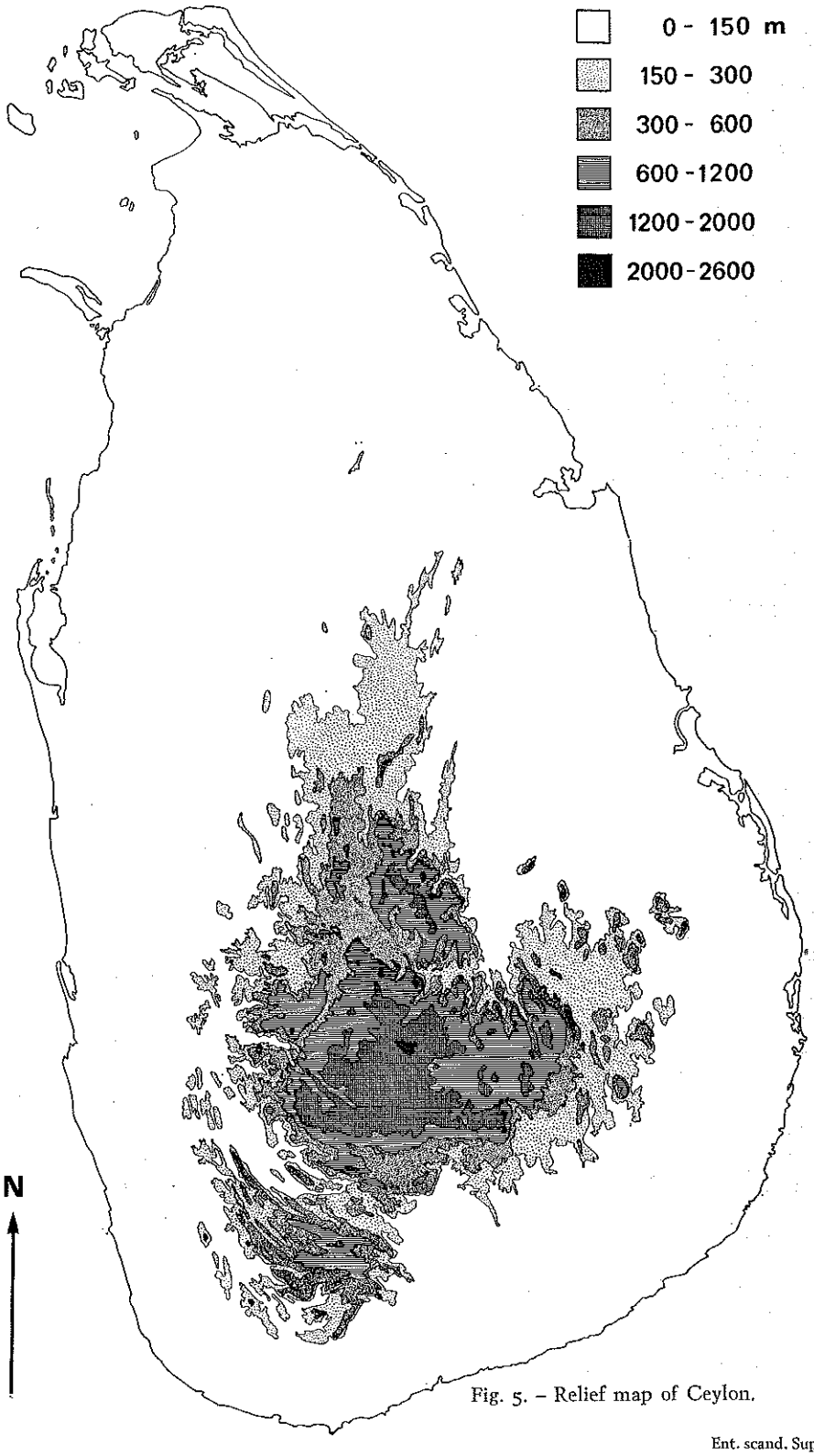

Fig. 5. – Relief map of Ceylon.

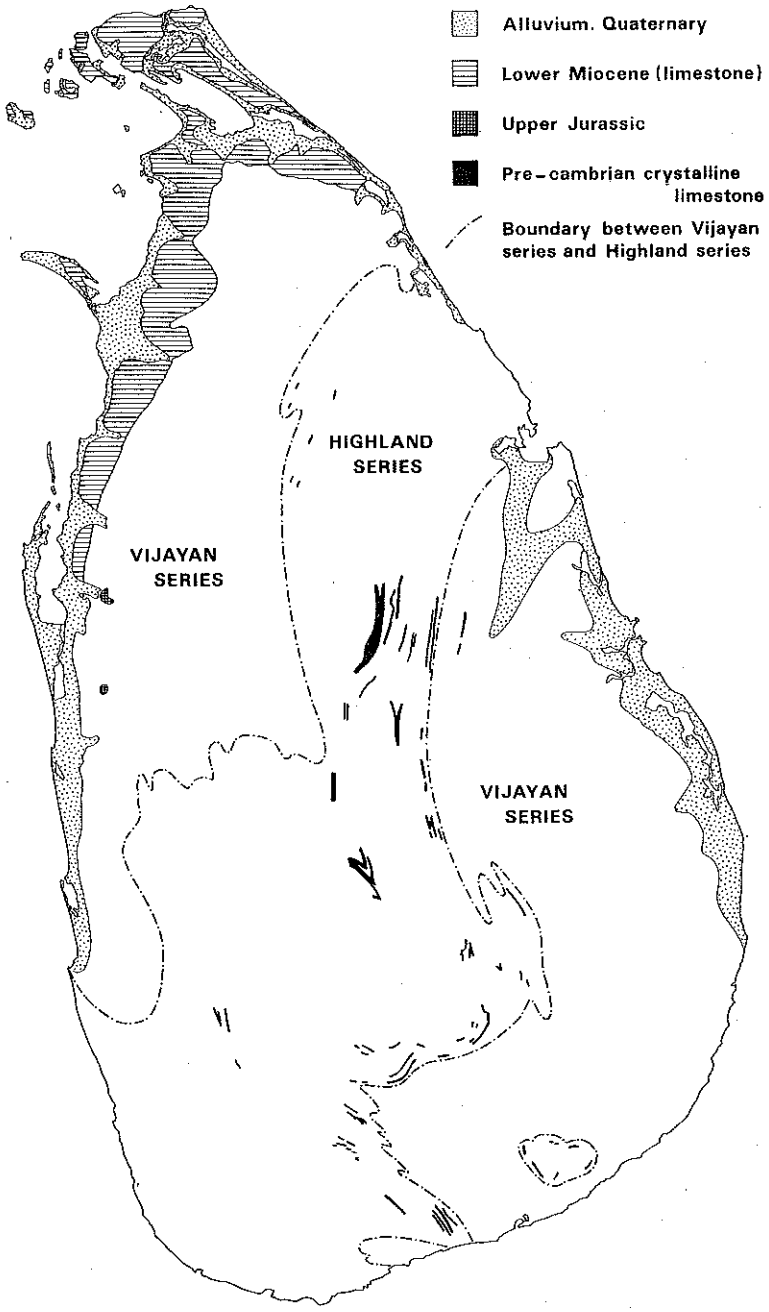

Fig. 6. – Geology of Ceylon. After Cooray 1967. Redráwn and simplified.

is given by Cooray (1967).

Alluvial soils, mainly sand, clay and silt, cover relatively large areas of Ceylon, particularly along the coast and at the outflow of the large rivers.

In the northwestern dry parts of the island red-yellow soils with a high cation exchange capacity are widespread on old coastal alluvia and on the miocene limestone.

The dominating soils in the dry zone (outside the area with 2000 mm rainfall) are reddish brown earths, derived from basic or neutral rock material. The upper horizons are brown, while a reddish horizon begins at some depth. On the acid gneisses of the southeast where there is a deficiency of ferromagnesian minerals non-calcic brown soils develop.

In the wet zone podsolic soils predominate, independent of the subsoil parent material. In the high altitude grassland (patana) and the fernlands there is a dark humic horizon, while laterization occurs particularly in the western part of the zone.

Soils of Ceylon were described in more detail by Moormann and Panabokke (1961).

2. Climate

Ceylon is situated within the equatorial belt of calms; the intensity and narrow amplitude of the insolation is an important factor controlling the climate. There are only slight seasonal variations in temperature, air humidity and day length.

The annual mean temperature at station level for a period of three decades was 27.2° C in the lowland (Colombo, Jaffna, Hambantota and Anuradhapura), 24.4° C in the upland (Kandy) and 15.4° C in the highland (Nuwara Eliya). The mean temperature of the months varies only slightly: the yearly amplitude is 1.7–1.8° C in the coastal lowland (Colombo, Hambantota and Anuradhapura), 2.7° C in the upland (Kandy) and 2.4° C in the highland (Nuwara Eliya). The coldest month December or January with about 26.1° C in the coastal lowland (Colombo), about 24.4° C in the interior of the lowland (Anuradhapura), about 23.3° C in the upland (Kandy) and 14.4° C in the highland (Nuwara Eliya). The narrow amplitude of the temperature is a result of the influence of the sea and the cloudiness which is often greatest at the hottest time of the day. Snow is almost unknown in Ceylon and night frosts are rare even at high altitudes.

Similarly the mean relative humidity varies only slightly in the year and between the months. For 30 years the annual amplitude at the coast in the lowland (Colombo) was 11 % in the day and 6 at night (68–79 % RH in the daytime and 87–93 % RH at night); in the interior of the lowland (Anuradhapura) the same figures were 18 and 7 (60–78 and 88–95), in the upland (Kandy) 16 and 7 (60–76 and 87–94) and in the highland (Nuwara Eliya) 24 and 5 (60–84 and 88–93).

Although Ceylon as a whole has a high rainfall and there is virtually no month without some rain, a considerable part of the island suffers from drought. Because of the very strong evaporation, the area outside the 2000 mm isohyet depends on artificial water storage for cultivation. In the southwest, "the wet zone" (with 2000 mm rainfall a year), there is ample rainfall all through the year, while in the rest of the country, "the dry zone", there is a dry season which may last several months in the north (Fig. 7).

The average annual rainfall varies from about 1000 mm on the northwest coast to more than 7000 mm (stations in front of Adam's Peak). Much of the rain is produced by the strong convection currents (sudden heavy showers or thunderstorms), less by migrating low pressures (drizzling followed by wind and rain). In June, July and August the southwest monsoon greatly affects the climate in the southwestern and central part of the country, while the northeast monsoon, in December, January and February, affects the northeastern lowland, upland and the adjoining flanks of the central highland. The amount of rain and the season for rainfall varies greatly, depending on the geographic position of the place and the relief of the country.

3. Terrestrial habitats

Although Ceylon is a comparatively small island (65,584 km^2), it is much more varied than is usual within the calm equatorial belt. The complex relief and rainfall pattern have generated a number of different biocoenoses. It is impossible here to describe or even indicate the wealth of habitats represented in the island. There are numerous man-made habitats

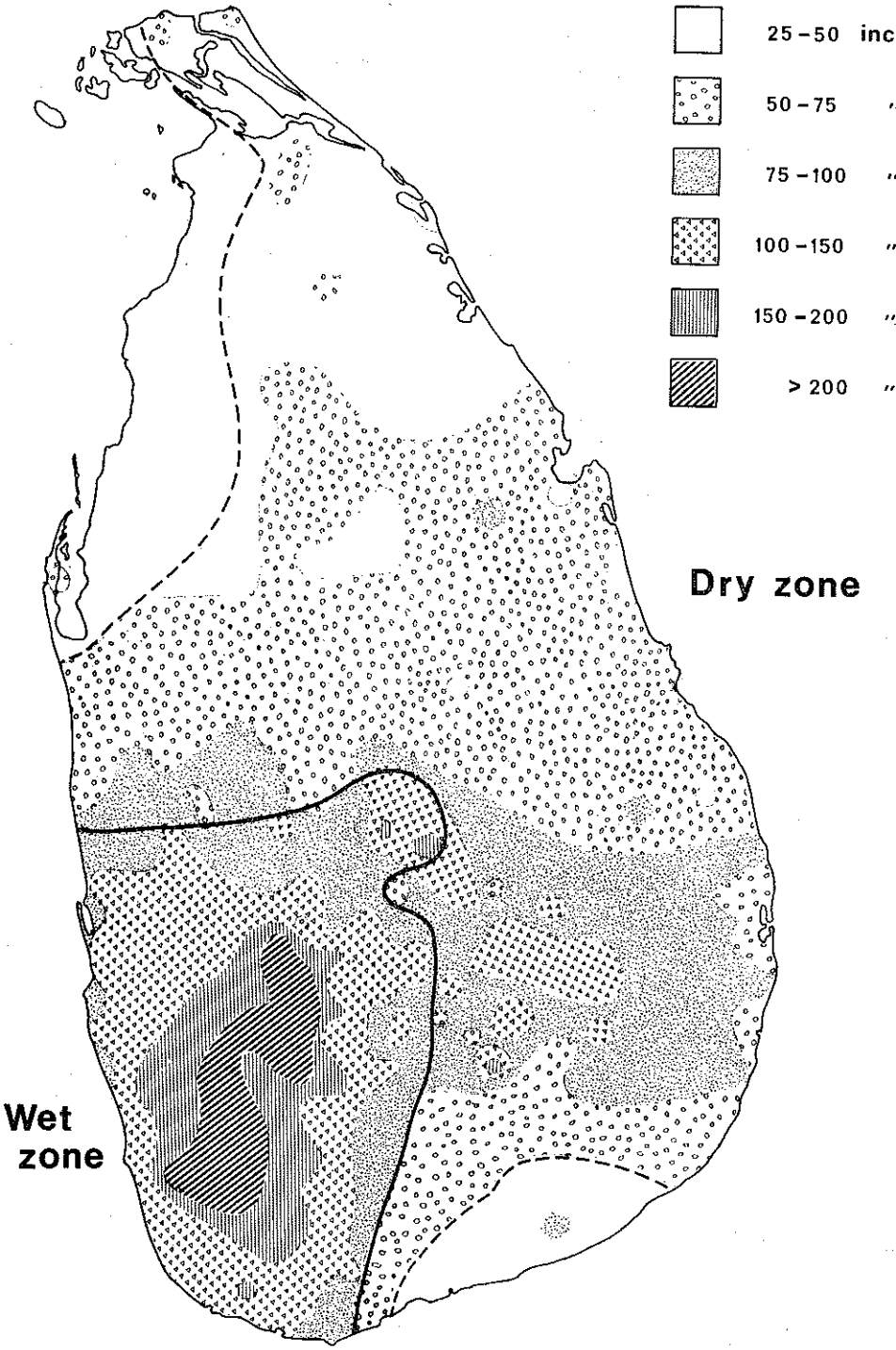

Fig. 7. – Annual rainfall in Ceylon, according to Rainfall Map 1955 of Survey Department, Ceylon. Thick line encloses the wet zone. Broken lines enclose the very dry areas in northwest and southeast.

and seres resulting from exploitation and conversion of the land through millenia. Only fragments are left of the original plant cover, in spite of the fact that only about 25 % of the island is at present cultivated (cf. Fig. 11). In ancient time the lowland was densely populated and movements of population from one part to another brought about heavy exploitation in the upland as well. All the lowland forest area, which is now sparsely populated in the dry zone, may at some time have been cultivated (cf. Figs. 9 and 10).

Present circumstances may be better understood, by surveying the generalized ecosystems, which should eventually develop, on the basis of the primary vegetation types, if human influence were to disappear. This has been summarized in map, Fig. 8 which also demonstrates the distribution of some of the important crops (tea, rubber, coconut) which have taken the place of much of the virgin evergreen forests of Ceylon. The map does not include open, coastal biocoenoses which cover small spaces. In some areas they are greatly changed or destroyed, like the mangrove, but many species resist even considerable diminution of their habitat.

1. The Dry zone Manilkara ecosystem covers the northwestern and southeastern lowland where annual rainfall ranges between 600 and 1200 mm. The vegetation is characterized by medium-sized semideciduous trees like the Ceylon ironwood *Manilkara hexandra* Roxb., Dub. and the Satinwood *Chloroxylon swietenia* DC. over a layer of spinous bush, and dense creepers. Much of the ecosystem is now changed, because of exploitation of the wood and cultivation or grazing. In many areas there is a secondary spinous dense scrub vegetation or a dry grassland, kept open by fire.— In Mannar island and surrounding areas the sandy soil has, besides *Manilkara* and *Bauhinia*, a sparse tree vegetation of *Acacia planifrons* W. & A.

2. The Dry zone Chloroxylon ecosystem covers much of the remaining lowland and parts of the upland. It may be doubted whether there are any large remains of primary forest in this area. Usually the secondary character is evident. In its old stages the forest is dense, dominated by a number of tall deciduous or semi-deciduous trees, e.g. the Satinwood *Chloroxylon swietenia* D.C., the Trincomalee wood *Berrya cordifolia* Burret, the Ceylon oak *Schleichera oleosa* Lour., Oken, and the evergreen Ebony *Diospyros ebenum* Koenig. Initially, exploitation means removal of the tall deciduous trees, often followed by shifting cultivation. The next, widespread stage is a dense shrub, less spinous and less dry than in the *Manilkara* ecosystem. As in the latter there are patches of grassland with scattered trees, dry savanna, kept open by fire.

3. The Intermediate zone ecosystem occupies peripheral parts of the wet zone lowland and wet upland to about 900 m above sealevel. Much of the area was cultivated in comparatively recent time and is now occupied by coconut plantations (cf. Fig. 8) or food crops. Most remaining forests are degraded or secondary. Clearing the forests in this area of high rainfall resulted in degeneration and erosion of the soil. In the secondary forest the humid and evergreen character is therefore less clear. In its climax stage the ecosystem is based on a tall forest (upper stratum at about 30 m) composed of numerous trees, many of which are evergreen, e.g. *Canarium zeylanicum* Bl., *Dipterocarpus zeylanicus* Thw., *Filicium decipiens* Thw., *Artocarpus nobilis* Thw. and *Euphoria longana* Lamk. The secondary forest is more transitional characterized by several of the species of the Dry zone Chloroxylon ecosystem. As a result of human interference certain areas are occupied by savanna, as usual with scattered trees resistant to fire.

4. The Lowland wet evergreen forest ecosystem originally covered the southwestern part of Ceylon to about 900 m above sea level. In this area the perpetual rainfall exceeds 2000 mm and the mean temperature of the two coldest months is 20° C. The virgin forests were composed of numerous evergreen tree species, some reaching heights of 40–45 m. There are very few remains of this, the foremost forest type of Ceylon (Fig. 8). The dominating trees are *Dipterocarpus spp., Doona spp., Vatica spp., Hopea spp., Shorea spp.*, and *Mesua ferrea* L. Exploitation and cultivation of this area of rainforest has degraded the soil. On exposed ground the humic layer was soon destroyed, the nutrient cycle broken and upwards movement of water during hot and dry days produced a lateritic cementation of layers near the surface. Uncultivated, deforested areas on mountain slopes are in places covered by fernland, mainly *Gleichenia linearis* Cl., or savanna.

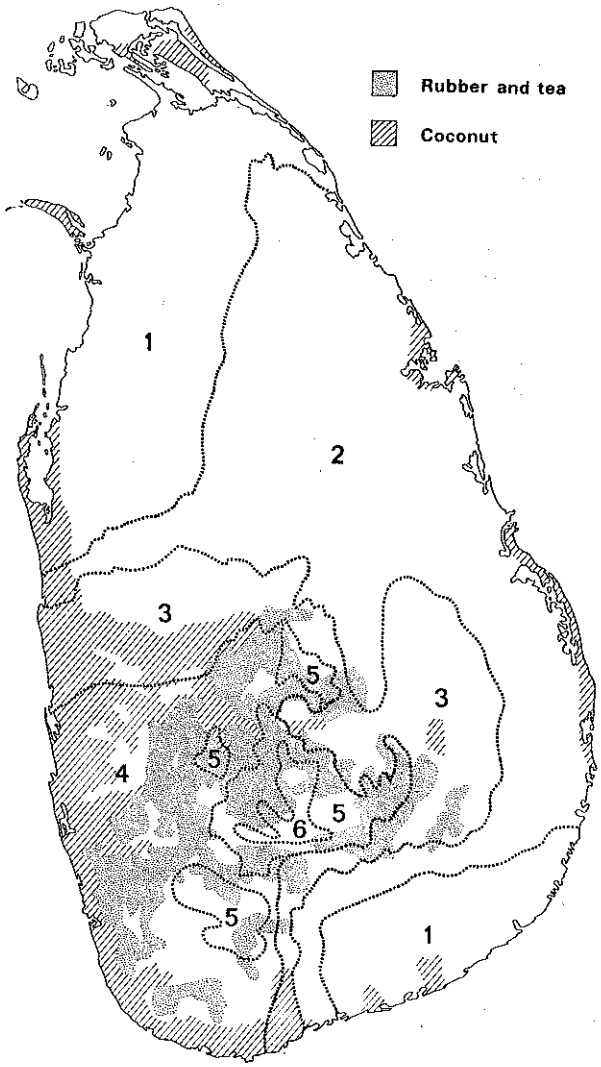

Fig. 8. – The distribution of generalized ecosystems of Ceylon. 1) The Dry zone Manilkara ecosystem. 2) The Dry zone Chloroxylon ecosystem. 3) The Intermediate zone ecosystem. 4) The Lowland wet evergreen forest ecosystem. 5) The Sub-montane wet evergreen forest ecosystem. 6) The Montane wet forest ecosystem.

5. The Sub-montane wet evergreen forest ecosystem occupies the area between about 900 m and 1500 m altitude in the wet zone. Although less productive than the Lowland wet evergreen forest, this ecosystem, transitional between systems 4 and 6, is composed of numerous tall species of trees, some of which are economically important, e.g. *Doona spp.*, *Calophyllum spp.*, and *Wormia triquetra* Rottb. Epiphytes are common. Deforestation has advanced far: grassland, "dry patanas", or "talawa", a type of savanna, and more recently plantations of tea, have occupied much of the area covered by the sub-montane wet evergreen forest (Fig. 8).

6. The Montane wet forest ecosystem covers the high altitude areas in Ceylon, above about 1500 m. The humidity and rainfall are

high and the temperature of the coldest months comparatively low. The low evergreen forest grows and regenerates slowly. Characteristic elements are e.g. *Syzygium spp., Gordonia spp., Michelia nilagirica* Zenk., and *Rhododendron arboreum* Sm. The trees usually bear mosses and lichens. Deforestation has resulted in the wet patanas, a grassland, at places with much *Pteridium aquilinum* L., Kuhn and scattered specimens of *Rhododendron arboreum*, adorned with *Usnea*.

Important details of vegetation and the change of nature in Ceylon are given in papers by De Rosayro (1950, 1958, 1961), Gaussen, Legris, Viart & Labroue (1965), Holmes (1958), Koelmeyer (1958), Eyre (1968) and in the Forest Inventory of 1961.

4. Inland aquatic habitats

As the greater part of the island consists of massive crystalline rocks, a large proportion of the rain runs off over the surface. There are many streams and rivers, particularly in the hill country where the rainfall is over 2000 mm and there are no or only a few dry months a year. In this broken area there is not a valley or depression without a stream. All types of running water are well represented: from water falls and cool mountain torrents with a sparse aquatic vegetation to warm slow-flowing and meandering streams and rivers, where aquatic plants may occur in great quantities. The fauna of the running water bodies is rich and varied, including many endemic taxa.

There are only a few large rivers in Ceylon, e.g. Mahaweli Ganga and Aruvi Aru,[1] but about a dozen medium-sized. Many of the smaller rivers and streams in the lowland dry up or are reduced to trickles from about June to September. On the other hand, they are liable to flood at the time of heavy rain during the monsoon periods.

In the hill country the stream and river bottom is rock or stone, while in the lowland banks of sand and mud are common. At the outflow into lagoons or into the sea there is often a delta land or a flat surface which may be of considerable size. Numerous such habitats are ideal for interstitial fauna, depending on salt (marine), brackish or fresh water.

There are many springs in Ceylon: a broad spectrum from fresh or brackish wells in the limestone area of the Jaffna region to the cool and clean rheocrenes of the forested central mountains. Hot springs occur at a number of places, e.g. at Kanniyai near Trincomalee (loc. No. 62). The fauna of the springs is not well known.

There are few, if any natural lakes in Ceylon (Fernando and Ellepola, 1969). Since ancient times series of tanks have been constructed in most river systems of the lowland, particularly in the dry and formerly densely populated northern and southeastern parts of the country (Figs. 9, 10 and p. XIII). These reservoirs (tanks) are called *wewa* in Sinhalese and *kulam* by the Tamils. According to Abeywickrema (1965) there are about 10,000 such reservoirs in Ceylon, the vast majority being rather small. The great number of such small man-made lakes may have greatly influenced the distribution of the freshwater biota of the lowland. There is a study of the fauna of some small reservoirs by Fernando and Ellepola (1969).

Rice (paddy) is grown almost everywhere in inhabited areas of Ceylon. The wet paddy covers about 1,500,000 acres (Ceylon Statistical Abstract 1963) and most is grown in well-irrigated alluvial plains or river valleys. Water from tanks or rivers is kept running over the paddy fields until they are drained for the ripening of the paddy. This man-made habitat has a rich and widespread aquatic fauna.

5. Land use

The consequences of the impact of man on his natural environment are greater in the tropics than in the temperate zone. Some knowledge of the course of man's interference is necessary to explain conditions in Ceylon today.

The exploitation of the environment in Ceylon may be divided into six periods:

1. The prehistoric period, until about 200 B.C.
2. The Sinhalese Dry Zone civilization. About 200 B.C.–around 1300.

[1] In Sinhalese *ganga* means large river, *oya* river and *ela* stream. The Tamil word for river is *aru*, and for stream *aruvi*.

3. The Sinhalese Wet Zone civilization. About 1300–1505.
4. The European trade regime 1505–1815.
5. The great plantation epoch 1815–1948.
6. Modern time 1948–.

1. The prehistoric period. — The early history of Ceylon is not known. Stone implements have been found in the gravel of river terraces. In 1919, Wayland found them be Pleistocene in age; Deraniyagala (1958) came to the same conclusion. Other traces of Stone Age people have been associated with early veddas, a pre-Dravidian tribe which still has descendants in remote parts of the island. Like the veddas the early people were hunters whose influence on their surroundings was slight and transient. The veddas were still Stone Age men when the first Indo-European (Aryan) people settled in Ceylon.

2. The Sinhalese Dry Zone civilization. — According to the great Sinhalese chronicle Mahavamsa (Geiger, 1912) written in the fifth century A.D. the first Aryan (Sinhalese) settlers came to Ceylon some centuries B.C. They were in the main an agricultural people and they brought the use of iron to the island. At the time the chronicle was written Tamils, a Dravidian stock of people, were invading Ceylon.

The first Sinhalese settlements were in the Dry Zone: in the north, Rajarata with Anuradhapura as its capital, and in the southeast, Runhuna (Rohana). The chief reasons for the extensive occupation of these areas were probably that the land was easily cleared and suitable for agriculture, particularly cultivation of rice. On the other hand the period of drought was fairly long and, as the population increased, had to be overcome by irrigation. The construction of systems of reservoirs and channels started in the second century A.D. and reached a high technical level in the fourth century. At this early time there were only minor settlements in the Wet Zone, mainly in the lowland at the Kelani Ganga.

Persistent invasions of people from south India moved the centres of Sinhalese populations southwards and in the fifth century three other areas grew in importance, viz. Sigiriya, Polonnaruva and Mantai. Gradually much of the lowland was placed under a well planned and extensive scheme of irrigation and it seems clear that already during the first millenium A.D. the primary forest had suffered greatly.

Prosperity continued until the reign of Magha (1214–1235) when destruction by invasion and war was so severe that no rulers who followed seem to have taken up the task of repairing the damages to the irrigation works. In the far north a Tamil kingdom at Jaffna took over. Under the pressure of the general political unsafety in the 13th century the Sinhalese capital was moved to the Wet Zone.

The abandoned Dry Zone was recaptured by the jungle and a considerable part is still covered by secondary forests where numerous ancient tanks and channels can be traced (Figs. 9 and 10). It is probable that the decreasing population and the exodus were not results of war and insecurity alone. The great number of tanks must have been excellent breeding grounds for the malaria mosquitos. Malaria raged in the Dry Zone until recently.

3. The Sinhalese Wet Zone civilization. — At this time the main centres of Sinhalese population were in the Wet Zone, in the lowland and the upland. In the upland the people cultivated their rice in the river terraces or in valley bottoms, and the mountain slope and upper hills were used for grazing or as a source of timber. In the 14th century towns were founded also in the highland, e.g. at Sri Pada (Adam's Peak). Finally, the capital was moved to Kandy which was for long the stronghold of the Sinhalese kings.

This period meant exploitation of the wet lowland and the accessible part of the upland. Still, however, the rain forests of the mountain flanks and much of the highland, including the montane forests, were virgin.

4. The European trade regime. — Foreign interest in Ceylon started in ancient times. Colombo was early the shipping centre for export (precious stones, pearls, spices), grasped at and at times controlled by adventurers of various nationalities. The occupation by the Portuguese in 1505–1658 and the Dutch in 1658–1796 was in the interests of trade and did not interfere much with the natural environment. The same applied to the early British occupation in 1796–1815. Plantation agriculture was restricted to the lowland and the Sinhalese way of life did not change much.

5. The great plantation epoch. — After a convention between the Kandyan

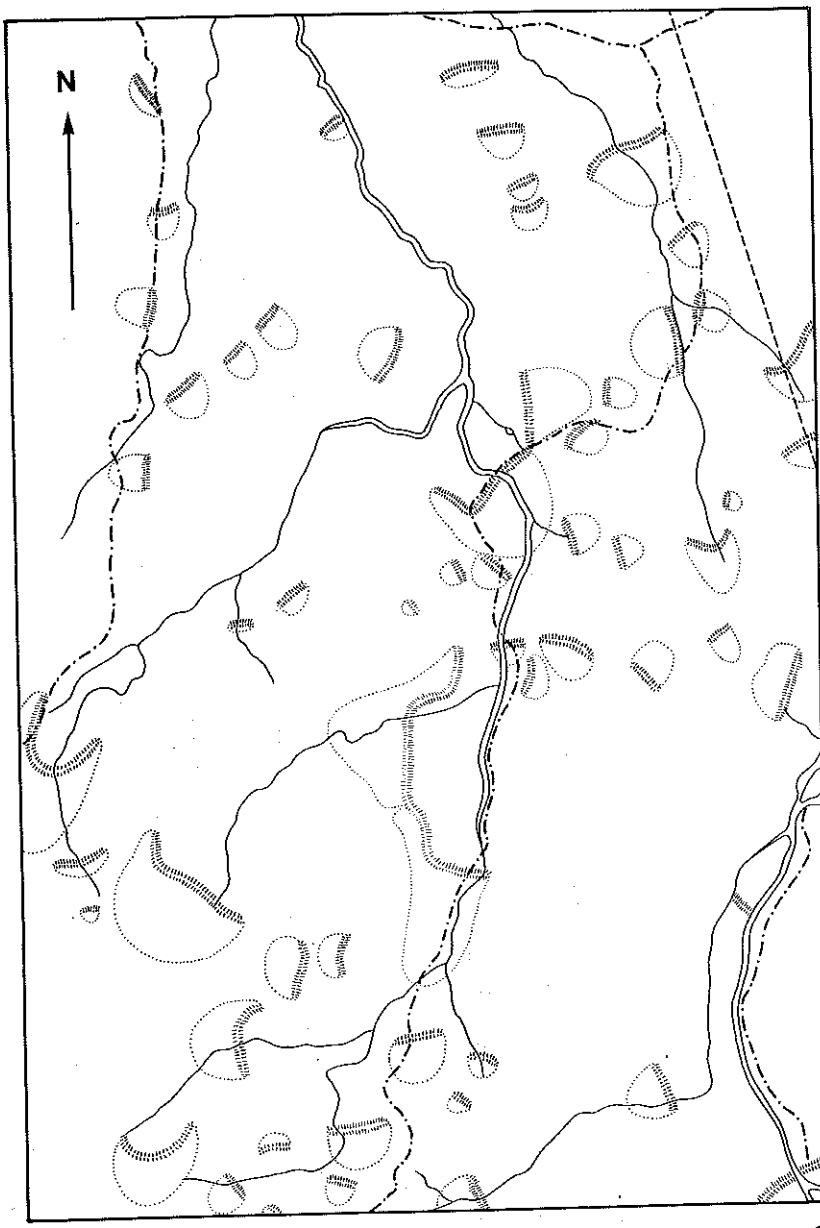

Fig. 9. – Ancient water reservoirs in Wilpattu National Park. – – – – national park boundary, – · – · – · old track. Drawn from One inch map of Ceylon, sheet C22,23, F2,3, 1958

Sinhalese chiefs and the British in 1815 the highland was opened up. Little by little the accessible parts of the highland were cleared and coffee or tea, later rubber, were planted. As labour supply was a problem, more than 900,000 individuals were recruited from south India in about 1850 for work in the plantations. At the end of the century the highland had changed greatly: roads made most parts accessible, plantation occupied considerable areas, and the forest disappeared correspondingly, while settlements were established at

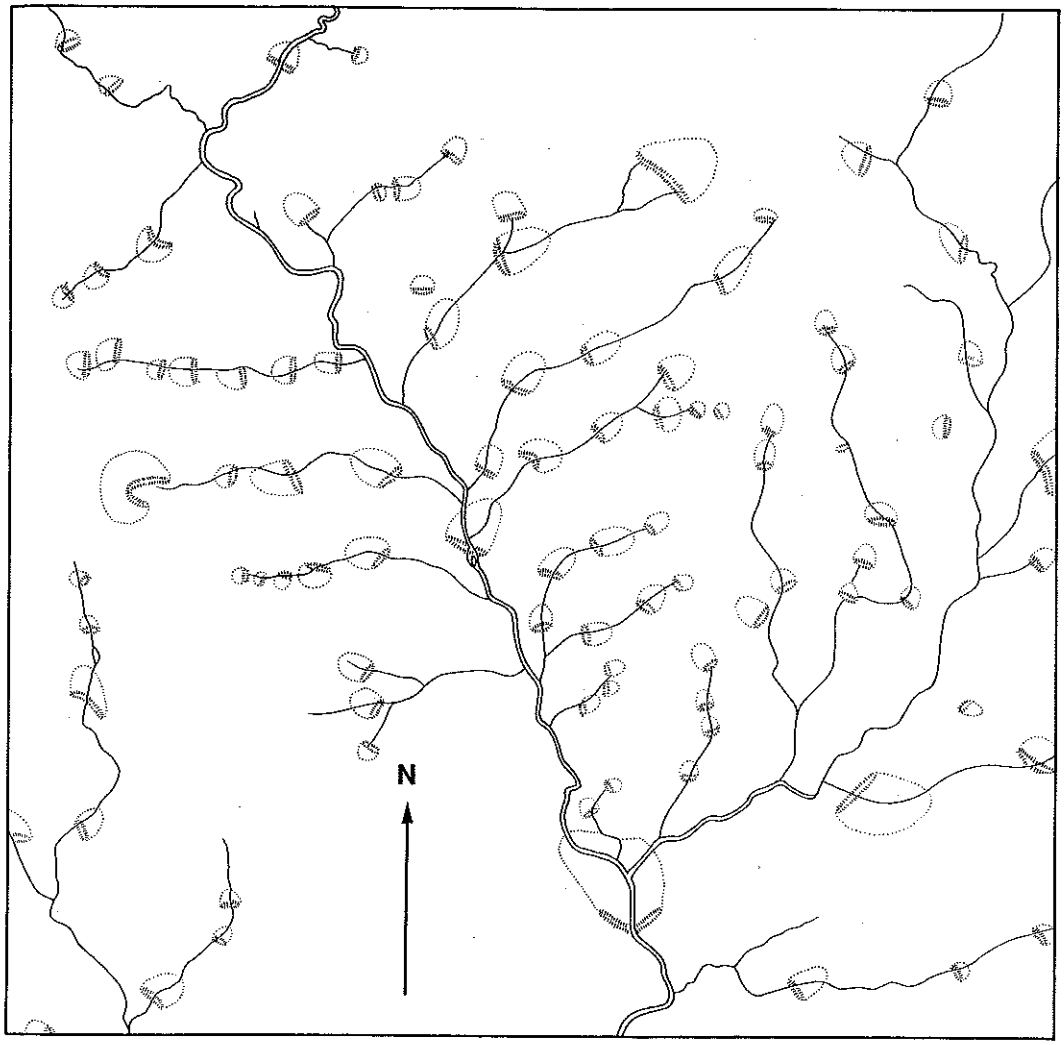

Fig. 10. – Ancient water reservoirs in the Mau Ara river basin in Wellawaya Division. Drawn from One inch map of Ceylon, sheet P1,2,6,7, 1962.

high altitudes. Plantations now cover a considerable part of the highland and the western Wet Zone (Fig. 8).

6. Modern time. — Since Ceylon gained its independence in 1948 the area of usable but uncultivated land has decreased rapidly. Now, there is hardly any such land left in the lowland Wet Zone and the upland. In the highland, exploitation of forest land has continued. During the British period there was hardly any development of the Dry Zone, where settlements were small and isolated and the land malaria-stricken. Since the conquest of malaria, re-colonization of the Dry Zone proceeds at an accelerated rate. But there is still a great difference in population density and cultivation between the provinces of the western Wet Zone and the dry provinces of the north, east and southeast (Fig. 11).

More details on the history of Ceylon, its people and natural resources, are given by Mendis (1947), De Silva (1953), and Farmer (1957, 1963).

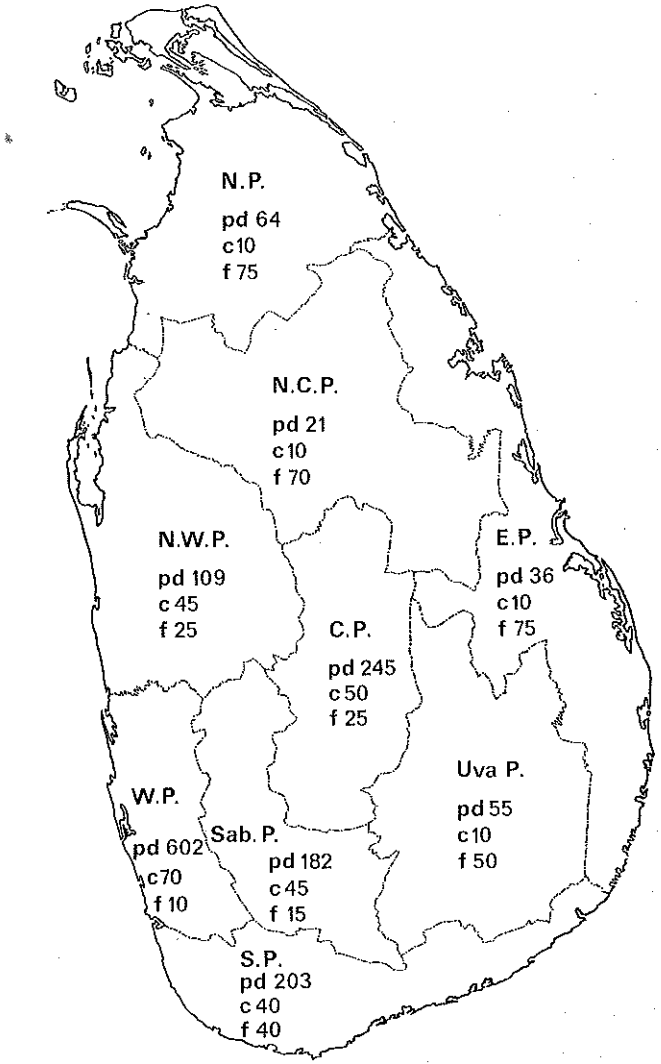

Fig. 11. – Provincial subdivisions, population density, percentage cultivated land and percentage forests in Ceylon. N.P. = Northern Province; N.C.P. = North Central Province; N.W.P. = North Western Province; E.P. = Eastern Province; C.P. = Central Province; W.P. = Western Province; Sab.P. = Province of Sabaragamuwa; Uva P. = Province of Uva; S.P. = Southern Province; pd = population density, inhabitants per kilometre^2; c = percentage cultivated land; f = percentage forests.

6. Itinerary of the Lund University Expedition in 1962

A complete list of the localities investigated is given below. A few introductory words may present the frame of our work.

The participants arrived in Colombo on 3.1.1962. Before leaving Sweden we had been informed that our voluminous equipment was being unloaded in Colombo. After our arrival it was found that the load dumped was potatoes from Sweden. Our ship was still in the roads because of a dock strike. A few days later the vessel sailed for Djibouti, where the

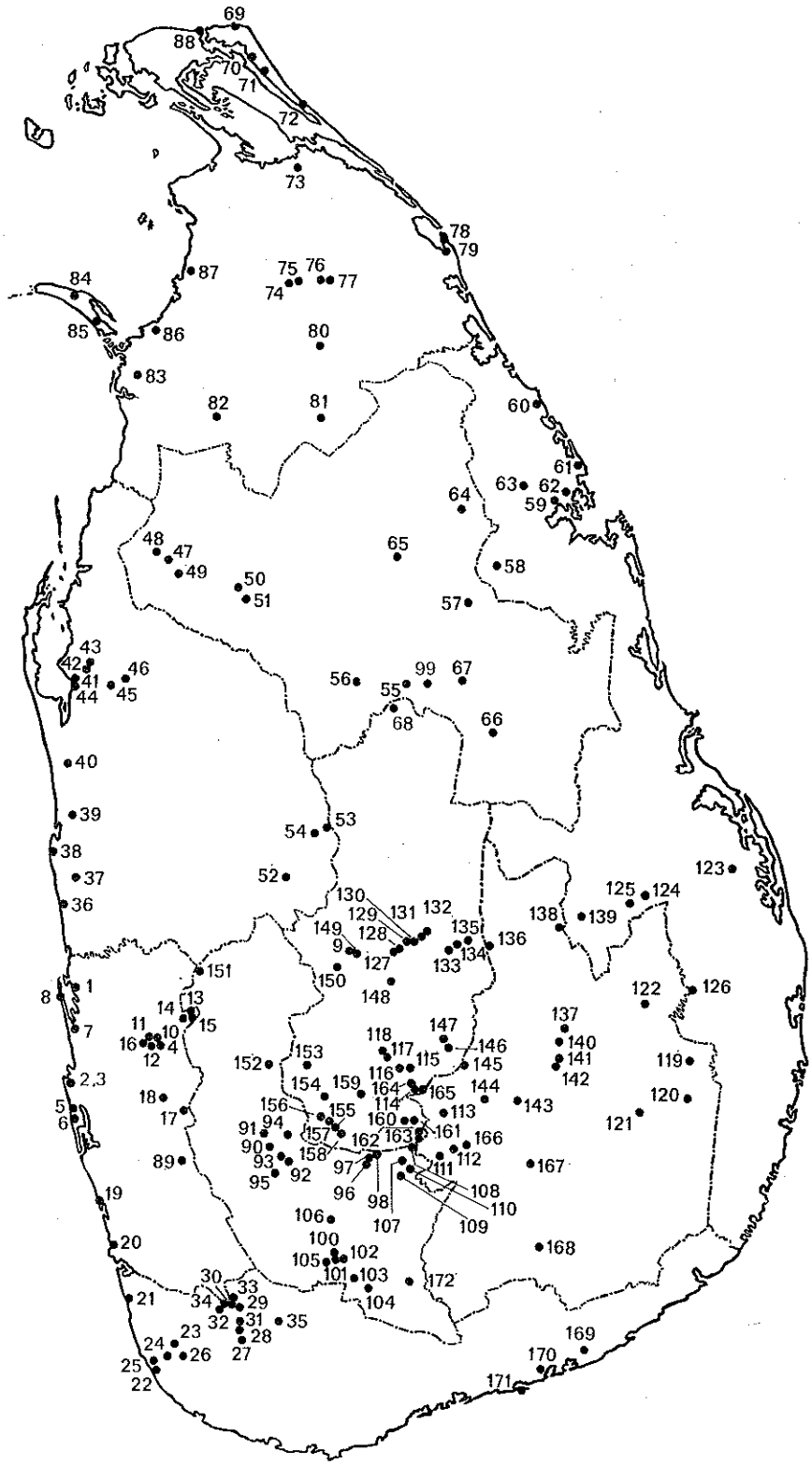

Fig 12. – Localities in Ceylon investigated by the Lund University Expedition in 1962. Cf. text pp. XXIII–XXXVI.

equipment was unloaded and stayed until it was returned to Sweden via Australia much later. In the meantime some boxes had been carried to Colombo by air and some spare equipment was sent from Europe. Subsequently, the supply became more plentiful. Our programme had to be modified and we concentrated on the ravine and freshwater fauna, particularly in the mountain areas. In the field we were accompanied by Mr Andrew Pereira, formerly of the National Museums, and at times by employees of the Department of Museums, besides local people.

Headquarters were established at Dambuwa Estate, near Yakkala in a magnificent old Sinhalese house. For the first weeks of work we used equipment on loan from the National Museums of Ceylon.

The geographic position of the localities investigated is indicated in Fig. 12. The provincial subdivision of the island is given in Fig. 11.

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