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# The Natural Landscapes of Central Canada

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**Abstract** Due to an unusual combination of climatic conditions resulting from the ameliorating influence of the Great Lakes and the intensification influences of Hudson Bay, there is a compression of life zones in Ontario in Central Canada. Within a distance of 1500 km, five major life zones or formations are found which have resulted in five natural landscape regions including southern deciduous forests, deciduous-evergreen forests, boreal forests, subarctic forests and subarctic tundra. The floristic, compositional and some of the ecological aspects of these landscape regions are outlined in this contribution.

In central Canada between the Great Lakes and James and Hudson Bays, there is a surprising variety of natural landscapes (Fig. 1) which includes an extensive number of vegetation communities (Macoun, 1894). These have developed under a number of significant environmental influences. The normal latitudinal effects which result in decreasing temperature, increasing severity of winter and decreasing duration of the growing season, are intensified in this region. Usually extensive bodies of water tend to ameliorate climatic conditions and this is true in respect to the Great Lakes, but not at all the case for Hudson Bay which in both winter and summer is a body of ice, not water. This has caused a strong suppression of life zones and thus over a distance of only 1500 km there occur 5 major formations which characterize the major landscape regions. From south to north, these are southern deciduous forests, deciduous-evergreen or mixed forests, boreal forests, subarctic forests and subarctic tundra, the latter a coastal fringe along Hudson and James Bays (Rowe, 1972). Another major climatic influence is related to the great inland prairies which have developed under an arid but continental climate. These influences have a strong impact on central eastern Canada and thus in northwestern Ontario there are significantly drier conditions which lessen in effect passing from west to east. This drier climate coupled with a strong warming period in the middle of the postglacial period, the so-called Xerothermic Period, has at different periods and under different influences, permitted the invasion of tallgrass prairies and related temperate savannas into northwestern and extreme southwestern Ontario.

Another environmental feature is of considerable impact on the natural landscapes of this region not only because of its indirect environmental influence but also because of its direct affects on visual aspects. This is the underlying geology of the region which includes limestone in the extreme south particularly in the Niagara Peninsula between Lakes Huron, Erie and Ontario, the granites of the extensive Canadian Shield and then again a broad expanse of limestone based territory in the Hudson Bay Lowlands which extends from the height of land between Mistassini-Timmins-Red Lake to the shores of Hudson and James Bays.

Three other influences have had a profound affect on the natural ecological systems of Central Canada. The influence of the great continental glacier is of major magnitude in the manner in which it moulded not only terrain, but also bedrock, and shifted materials from place to place. These effects are often considered to be in the far distant past but this is not actually the case. It is known that the great ice sheets receded from extreme southern Ontario about 12,000 years ago but areas adjacent to James Bay may still have been ice-covered as little as 3000 years ago, a relatively short span of time. The great weight of ice caused a strong depression of this latter terrain and the ground has been rising because of isostatic rebound at the rate of about a meter per hundred years. The coastal areas are barely above sea-level so this rebound is exposing new

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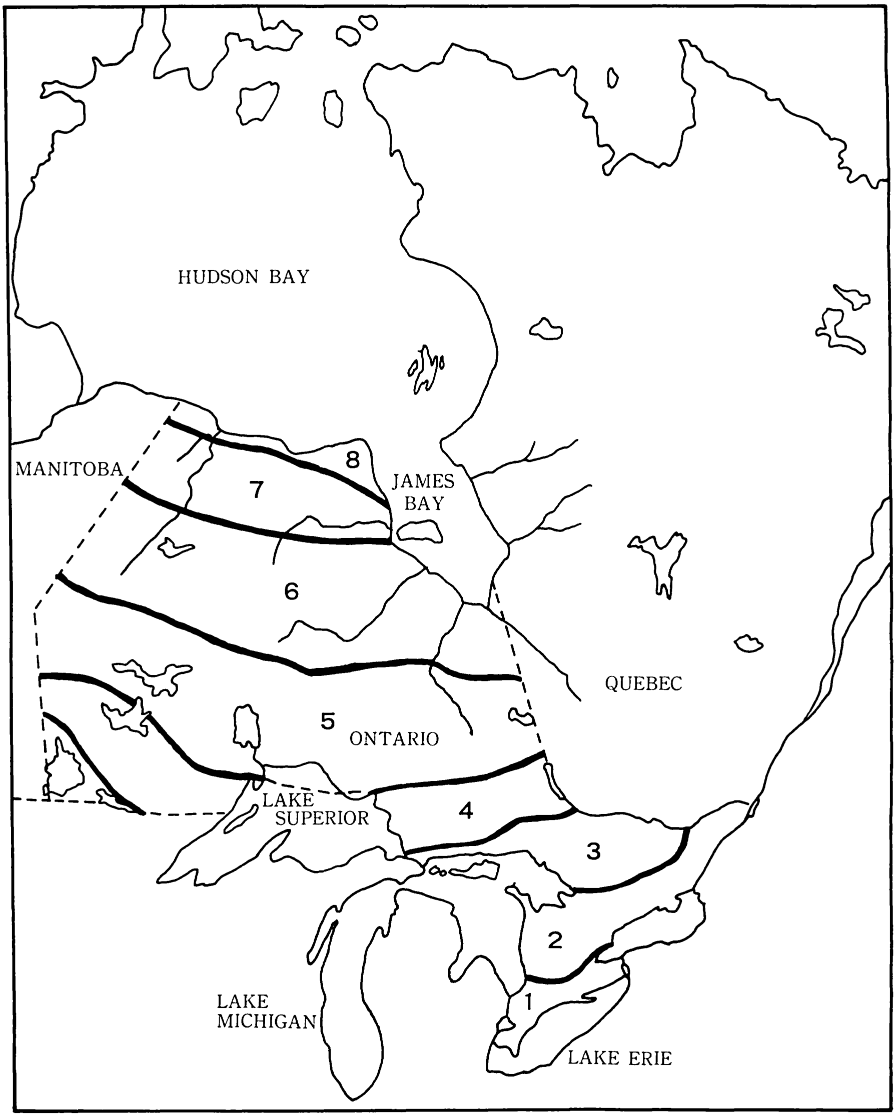

**Fig. 1.** Map of central Canada, principally the province of Ontario between the Great Lakes and Hudson and James Bays portraying the distribution of the five major landscape regions, 1: Southern Deciduous Forests, 2 and 3: Deciduous Evergreen Forests(southern and northern), 4,5 and 6: Boreal Forests (southern, central and northern), 7: Subarctic Forests and 8: Subarctic Tundra.

ground rising from the sea at a very significant rate. The second influence is fire. The native Indian is known to have had a strong influence on natural vegetation in setting fires to drive game, to clear land, to manage vegetational systems- blueberry barrens as an example, and to produce open terrain in an environment which was solidly ensconced in forest. Recently it is known that natural fires due to lightning have also been important in changing vegetation particularly in the drier northwestern region of the boreal forest. The last impact has perhaps been one of the strongest- that of European man in the settlement of the continent. At the beginning natural vegetation had to be cleared to produce arable land for survival and man surmised that the forest was an enemy. Four hundred years have passed and in each century new technology has developed to assist man in waging this battle. He still does not seem to realize that he now has total mastery over the forest and can ultimately decide its fate.

Each natural landscape region is an expression of the regional landforms and their variable features from locality to locality, with the associated vegetational communities. They are identified in reference to the predominant vegetation which is the resultant of regional climate, geology, soils and biological interactions.

### 1. The Southern Deciduous Forests Landscape Region

This region is underlain by limestone and is relatively flat with one major exception. Beginning at Niagara Falls, in fact responsible for the great cataract of the falls, is the Niagara Escarpment. At its highest it is only several hundred meters but it passes west for about 65 km and then veers northwest across extreme southern Ontario and forms the extensive Bruce Peninsula between Georgian Bay and Lake Huron and then Manitoulin Island, which is the largest freshwater island in the world. The ridge of the Escarpment has very shallow soils and bedrock emerges frequently especially on the Bruce Peninsula and Manitoulin Island. Areas adjacent are very scenic because the escarpment breaks the extensive flatlands and the dry shallow soils allow forests composed of drier components to develop (Chapman and Putnam, 1943).

The forests of the entire region develop under five site moisture conditions-dry, dry-mesic, mesic, wet-mesic and wet (Maycock, 1963). Dry and dry-mesic are on upland severely drained sites whereas mesic conditions prevail where there is optimum supply of moisture but with good drainage and no waterlogging. Wet-mesic sites have excess water seasonally and drainage begins to be impeded whereas wet areas often have standing water in spring and after extensive rains throughout the year. Wet-mesic and wet conditions may develop in two situations- lowlands or bottomlands.

The landscapes of this region are composed predominantly of deciduous broadleaved summer green forests and occur on flat or flat to rolling terrain. Mixed deciduous-evergreen forests are uncommon but may be found on sandspits and sand plains along the shores of the Great Lakes and in isolated areas along and adjacent to the Niagara Escarpment. There are about six localities where very restricted relict coniferous bog forests have persisted since glaciation. In the extreme southwest there are still tallgrass prairies and associated savannas but these have been used extensively for agriculture as have most of the deeper mesic, wet-mesic and dry-mesic forest sites. Along the shores of the Great Lakes there are extensive sand dune communities and meadows, marshes and aquatic systems fringe the very wet, saturated and open water habitats of the embayments, as well as line the rivers and streams.

In this region there are about 85 different tree species which form the forests; only six are coniferous and two of these are found exclusively in relict bogs (Macoun, 1893). Despite this large number, only four trees are of major importance in forming the forests- *Acer saccharum, Fagus grandifolia, Quercus rubra* and *Ulmus americana.* Trees of secondary importance which can also be forest dominants are *Acer saccharinum, A. rubrum, Carya cordiformis, C. ovata, Fraxinus americana, Juniperus virginiana, Quercus alba, Q. macrocarpa, Q. palustris, Q. velutina* and *Salix nigra.* A few additional trees may be locally dominant: *Celtis occidentalis, Juglans nigra, Pinus strobus, Platanus occidentalis, Populus deltoides, P. tremuloides, Quercus bicolor, Salix amygdaloides, Tilia americana, Tsuga canadensis* and *Ulmus rubra.* Within this region a large number of trees attain northernmost limits in eastern North America and are usually of minor importance in forest systems (Fox and Soper, 1952, 1953, 1954; Soper 1955). Some of these are *Asimina triloba, Carya ovalis, C. glabra, C. laciniosa, Castanea dentata, Cornus florida, Fraxinus quadrangulata, Gleditsia triacanthos, Gymnocladus dioica, Juglans nigra, Liriodendron tulipifera, Magnolia acuminata, Morus rubra, Nyssa sylvatica, Platanus occidentalis, Pyrus coronaria, Quercus muehlenbergii, Q. palustris* and *Sassafras albidum.*

The dry forest systems are composed mainly of species of *Quercus* and of the nine present in central Canada, *Quercus rubra* and *Q. velutina* are most significant. *Q. alba* is also present and can dominate stands while *Q. macrocarpa* is much less significant. *Quercus velutina* occupies the driest sites on sandplains and is dominant in combinations with *Q. rubra, Q. alba, Acer rubrum, Juniperus virginiana* and *Cornus florida. Quercus rubra* is also a dominant on sandy soils with *Q. alba, Q velutina, Pinus strobus* and *Fagus gran-*

*difolia. Quercus alba* is dominant on dry sands and on loams and even clays. It is dominant with *Q. rubra, Q. velutina, Carya ovata* and *Pinus strobus. Pinus strobus* may occasionally be dominant on sandplains and on rocky or naturally eroded sites on steep slopes and promontories along the Niagara Escarpment. On sandspits and rock outcrops *Juniperus virginiana* may be dominant locally. *Acer rubrum* is locally dominant on dry loams and *Carya ovata* on rock outcrops and dry clay sites. In southwestern Ontario under dry conditions there was frequent occurrence of temperate savannas dominated strongly by *Quercus velutina. Quercus alba, Q. muehlenbergii* and *Q. rubra* are secondary oaks of much lower levels of importance. Associated with these savannas (Fig 2) locally there is or was almost consistently, extensive tallgrass prairies composed of *Andropogon gerardi* and *A. scoparius* as major dominants as well as a large number of grassland forbs and shrubs (Fig. 3).

The dry-mesic forests have a much greater variety of tree species, much more compositional variation as well as much more variation in dominance patterns. *Acer saccharum* has a very broad amplitude of tolerance to moisture and to soils and it with *Fagus grandifolia* is dominant in a majority of sites. *Acer saccharum* dominates in combination with *Quercus rubra, Q. alba, Fagus grandifolia, Fraxinus americana,* and *Acer rubrum. Fagus grandifolia* is a dominant in forests with *Acer saccharum, Quercus rubrum, Fraxinus americana* and rarely *Pinus strobus. Quercus rubra* is also a major dominant in dry-mesic environments and is associated with *Q. alba, Acer saccharum, A. rubrum* and infrequently *Quercus macrocarpa. Quercus alba* is also found as a forest dominant on sand but moreso on loam soils and occurs in combination with *Q. velutina, Q. rubra* and uncommonly with *Liriodendron tulipifera.* On warmer sandspits *Celtis occidentalis* is infrequently locally dominant occurring with *Juniperus virginiana, Fraxinus americana* and *F. quadrangulata. Pinus strobus* is also locally dominant particularly on the southern lakeshores and sandspits with *Quercus rubra* and *Q. velutina.* Along the Niagara Escarpment on sandy north facing slopes *Tsuga canadensis* can be a dominant with *Pinus strobus* and *Fagus grandifolia.* A number of other trees also dominate forest stands but are infrequently encountered. These include *Ulmus rubra, Juniperus virginiana, Acer rubrum, Tilia americana* and *Carya ovalis.*

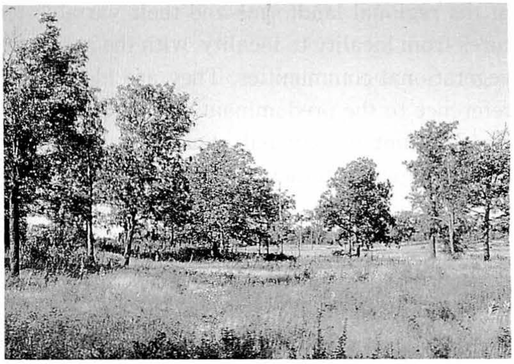

**Fig. 2.** Temperate savanna on dry shallow soils over limestone near Trenton, Ontario. *Quercus macrocarpa* and *Carya ovata* are the major dominants.

**Fig. 3.** Mesic tallgrass prairie dominated by *Sorghastrum nutans* and *Andropogon gerardi.* Walpole Indian Reservation, Lambton County, southwestern Ontario.

Growing under these dry-mesic conditions forest communities predominate. There are a few savannas and prairie systems in the extreme southwest which contribute visually to the landscape but other vegetation types are uncommon. The temperate savannas produce an unusual landscape much different than forests. They have open-grown broad crowned trees widely spaced and at much lower densities than forests. The dry-mesic savannas are dominated strongly by *Quercus velutina* and *Q. alba* is the only other tree of any importance. Perhaps the only significant exceptions are deciduous-evergreen forests and inclusions which are frequently associated with the rocky and steep slope habitats of the Niagara Escarpment.

Comments such as those presented above about the scarcity of communities other than forests on

**Fig. 4.** Old growth southern deciduous mesic forest dominated by *Acer saccharum* with *Tilia americana* and *Ulmus rubra*. Niagara Escarpment, St. Catherines, Ontario.

dry-mesic sites can be even more strongly stated for mesic sites. With the rare exceptions of deciduous-evergreen forests and inclusions along the Niagara Escarpment, mesic sites are most favourable for deciduous forests and they are most strongly dominant in these situations.

In mesic environments *Acer saccharum* is the overwhelming dominant (Fig. 4). It finds these conditions most favourable and is highly successful in forming forests and in perpetuating itself there. The most frequent associate of *Acer saccharum* is *Fagus grandifolia* which attains ecological optima in both dry-mesic and mesic sites although it is probably more so in dry-mesic. *Fraxinus americana* is also a strong associate in stands dominated by *Acer saccharum,* but other less significant co-dominants include *Acer nigrum, Liriodendron tulipifera, Ulmus americana, Carya cordiformis, C. ovata, Ulmus rubra, Tsuga canadensis* and *Pinus strobus.*

*Fagus grandifolia* is less than half as important as *Acer saccharum* but it is often a dominant on loam soils with normal microclimate on flat to gently rolling land. The most frequent co-dominant is *Acer saccharum,* but *A. rubrum* and *A. nigrum* are also found with the species. The only other significant dominant on mesic sites is *Tsuga canadensis,* most often occurring in colder than normal microclimatic north or east-facing slopes or in ravines, often along the Niagara Escarpment. It can be associated with *Pinus strobus* another conifer, but most often with *Acer saccharum.* Similar forests dominated by *Pinus strobus* in comparable localities have *Quercus rubra, Q. alba* and *Fagus grandifolia* as associates.

There are a number of other trees which can dominate forests on mesic sites although this occurs infrequently. More often they are associated with other dominant species. These include *Quercus rubra, Q. macrocarpa, Acer rubrum, A. nigrum, Ulmus rubra* and *U. americana.* The last mentioned species is a major dominant at the moist and wet end of the moisture continuum and it is very frequent as an associate or subdominant in mesic and wet-mesic forests.

Savannas on mesic sites are less widespread than those in drier or wet environments. *Quercus velutina* is a very strong dominant while *Q. alba* and *Q. palustris* are only of moderate influence and *Q. macrocarpa* and *Carya ovata* offer minor contributions to the tree layer. Mesic prairies are found but are not as widespread as drier and moister types.

Wet-mesic environments which occur in lowland depressions and lower slopes contribute very strongly to the present landscapes of the deciduous forest and will increasingly contribute as upland forests are diminished by continued clearing. Such forests are very rich in species and many trees contribute to the canopy layer. Outstanding is the dominance exerted by *Ulmus americana* and the strong influence of *Acer saccharum* which continues from mesic environments. Associated with *Ulmus americana* again are a number of co- or subdominants including *Fagus grandifolia, Quercus rubra, Acer saccharum, A. rubrum, A. saccharinum, Carya cordiformis, Fraxinus pennsylvanica* and *Salix nigra.* Associated with *Acer saccharum* are *Fraxinus americana, Quercus rubra, Fagus grandifolia, Ulmus americana* and *Acer negundo,* mostly as subdominants.

Of the many other trees which can dominate various soil and microclimatic environments under wet-mesic moisture conditions, *Quercus macrocarpa* and *Tsuga canadensis* were found in three situations sampled, *Pinus strobus, Betula papyrifera, Fagus grandifolia, Carya cordiformis, Acer negundo* and *Quercus palustris* were found in two, and eight others were found in just one. Thus the variation in composition and structure of wet-mesic stands is highly variable even from the point of view of major dominants and subdominants. The soil sites which support the richest assortments of stands are the loams and clays, particularly the latter and this is not surprising because of their high water retaining capacity and poor drainage features.

Such sites also provide environments for a number of savanna systems as well as associated wet-mesic prairies and tall shrub thicket communities. In the savannas *Quercus palustris, Q. macrocarpa* and *Q. bicolor* are the major trees with *Q. velutina, Carya ovata* and *C. laciniosa* as associates. In the prairies *Spartina pectinata, Calamagrostis canadensis, Andropogon gerardi, Panicum virgatum* and many forbs, are significant dominants or contributors.

The deciduous forests which are found in wet environments are the richest and most variable of all the landscape regions of central Canada. This richness is related to the tremendous ecological opportunities which are afforded these systems by the favourable climate, variety of soils, and also by the great differences which exist within the environments which can be included here. The major differences relate to topographic situations which strongly influence total moisture supply, flooding, drainage, nutrient supply, aeration and flushing. There are two main types, one is lowlands - depressions in the landscape which collect water after snowmelt or rainfall, and it sits and drains very slowly or is dissipated by transpiration or evaporation. Aeration in these soils is poor. The other situation is bottomlands - on river terraces occurring at different levels above the adjacent water systems. These are extensively and often deeply flooded at spring runoff, then they drain, but may again be flooded in the event of major rainstorms, even during the active growing period. These sites are generally well aerated and very fertile.

A total of 23 dominance patterns for the many tree species occurring in these forests has been found. Of these the majority, 16, occur in lowlands and 7 in bottomlands. The latter sites although seemingly very favourable, are probably the most stressful, and the deep, lasting flooding which may occur, although temporarily, is probably the most different. Of the lowland forests, a number of dominance patterns are found restricted to wet organic substrates or organic overlying sand: *Larix laricina, Picea glauca, Thuja occidentalis, Tsuga canadensis, Populus tremuloides, Betula papyrifera and Betula lutea,* whereas others are found mainly on loams and clay: *Acer saccharinum, Ulmus americana, Acer rubrum, Quercus macrocarpa, Q. bicolor, Fraxinus americana, F. pennsylvanica, Quercus palustris* and *Nyssa sylvatica.* Of all of these, those dominated by *Ulmus americana* and *Acer saccharinum* are most numerous and widespread. These species are by far the most significant dominants of all lowland ecosystems. The spread of the introduced Dutch elm disease, has been particularly devastating because populations of *Ulmus* were so abundant and widely distributed. The co-dominants of *Ulmus americana* dominated stands are mainly *Acer saccharinum* and *A. rubrum,* but *A. negundo, Quercus macrocarpa, Fraxinus americana* and *Betula lutea,* also occur. *Ulmus americana* is the most frequent associate in *Acer saccharinum* dominated lowland forests but *A. rubrum, Fraxinus pennsylvanicum, F. americana, F. nigra,* and *Betula lutea* are also found in this capacity.

In bottomland forests the dominance of *Salix nigra, S. amygdaloides* and *Populus deltoides* occurs most often, but that of *Salix alba, S. fragilis* (both introduced), *Acer negundo, Ulmus rubra* and the southern *Platanus occidentalis,* is also found. The most frequent associates in *Salix nigra* dominated stands are *S. amygdaloides* and *Acer negundo,* whereas in *Salix amygdaloides* dominant stands *Populus deltoides* and *Acer nigrum* have occurred. The other dominance patterns are too numerous to include here.

It should be added that the lowland coniferous dominated forests mentioned early in this section are predominantly the lowland relict boreal conifer bog systems which are found in the remnants of glacial lakes and potholes. Those not coniferous or mainly coniferous, including those dominated by *Betula papyrifera, Populus tremuloides, Betula lutea* and *Acer rubrum,* are advanced successional stages in such environments. The wet lowland and bottomland and the adjacent very wet environments provide sites for the development of many wet thicket systems dominated by numerous shrub species including

*Salix rigida, S. interior, S. lucida, S. petiolaris, S. discolor, S. bebbiana, Cephalanthus occidentalis, Cornus stolonifera, C. obliqua, C. racemosa, Spiraea latifolia, Alnus rugosa, Rhamnus alnifolia,* and many others. As the environments become increasingly wet to very wet, saturated and then open water, many different marsh, fen, sedge meadow, and aquatic systems begin to form an essential part of the landscape. These are too varied and numerous to be mentioned here but as examples, marsh systems may be dominated by *Typha latifolia, T. angustifolia, Scirpus acutus, S. validus, Phragmites communis, Zizania palustris, Calamagrostis canadensis, Sparganium eurycarpus, Cladium mariscoides, Eleocharis quadrangulata, Carex aquatilis, Pontederia cordata,* etc., many which occur or have ecological equivalents throughout the Japanese Archipelago.

## 2. The Deciduous-Evergreen Forests Landscape Region

The Deciduous-Evergreen Forests are often referred to as the Mixed Forest Region (Maycock and Curtis, 1960) because of the admixture of deciduous and coniferous tree elements. Others have also referred to this as the Northern Conifer Hardwood Region or the Great Lakes-St. Lawrence Region (Nichols, 1935; Frothingham, 1915; Halliday, 1939), all emphasizing the strong admixture of deciduous and needle-leaved trees. The mixed forests begin well south of the southern boundary of the granitic Canadian Shield or even the region where much granitic drift was deposited over the southern limestones. It is even important on the limestone based substrates of the Bruce Peninsula and Manitoulin Island. Thus it seems quite clear that these mixed forests are a response to increasing cold, particularly late frosts in spring, and a shorter growing season, conditions which seem to favour the coniferous over the deciduous habit. This is reinforced by the occurrence of coniferous dominated or mixed forests on colder north or east-facing slopes and in moister colder valley bottoms affected by cold air drainage, as well as by the much higher incidence of deciduous dominated stands on ridge crests and south as well as west-facing slopes. Throughout the whole region of discussion in fact, microclimatic situation due to topographic position resulting in normal climates on flat to mildly undulating terrian, warmer than normal on slope summits, south and west facing slope aspects, and colder than normal on north and east-facing slopes and in valley bottoms, is a major factor strongly influencing forest composition (Hills, 1958, 1959).

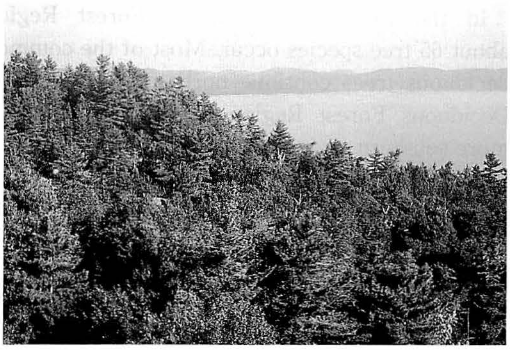

**Fig. 5.** General view of drier deciduous-evergreen forest on granitic bedrock with *Pinus strobus, P. resinosa* and *Acer saccharum.* East shore of Lake Superior, Agawa Bay, Ontario.

In the southern areas of this region deciduous dominated forests are more common than conifer dominated, and this slowly changes northward particularly in the granite bedrock region where the soils become considerably more acid (Fig. 5). As well northward, boreal coniferous trees are able to become established due to colder climates and successfully compete with deciduous trees and thus *Abies balsamea, Picea glauca, P. mariana, Larix laricina* and *Pinus banksiana* become contributors to the landscapes. The moisture features of sites also become more pronounced because on granite based sites the soils are often more shallow and underlying depressions in the bedrock maintain water levels much more effectively than sandy or clay soils. Thus the areas occupied by northern swamps are much more extensive. Because the granite bedrock in valley bottoms is not so gradually cut as the southern limestones, bottomland terraces along the rivers and thus bottomland forests are much less common. The incidence of natural fires here is also high and this has resulted in more conifer dominated forests particularly on rocky ridges and on severely drained sandplains, as well as more secondary successional forests dominated by *Populus tremuloides, P. grandidentata,* and *Betula papyrifera.*

In the Deciduous-Evergreen Forest Region about 65 tree species occur. Most of the common deciduous trees continue north of the Southern Deciduous Forest Region but those typical of more southern regions drop out relatively quickly toward the northern limit of deciduous forests. Of the trees there is an increase in the number of conifers, 12 in all, and then somewhat farther north the boreal conifers begin to establish on uplands and not just in lowlands or in relict conifer bogs.

Trees of major influence in the forests of this region include *Acer saccharum, Pinus strobus, Quercus rubra, Thuja occidentalis* and *Ulmus americana.* As well three species become very important area-wise and also in terms of the roles played in the post-fire successional development of many forests. These are *Populus tremuloides* and *Betula papyrifera* throughout the region and *Pinus banksiana* in the northern granitic areas. Trees of secondary influence in forest structure and composition are *Acer rubrum, Betula lutea, Fagus grandifolia, Fraxinus americana, F. nigra, Larix laricina, Ostrya virginiana, Pinus resinosa, Populus grandidentata, Quercus alba, Q. macrocarpa, Salix nigra, Tilia americana* and *Tsuga canadensis.* Certain trees are important only in specialized environments or are just locally significant. These are *Acer nigrum, A. saccharinum, Betula populifolia, Carpinus caroliniana, Carya cordiformis, C. ovata, Celtis occidentalis, Fraxinus pennsylvanica, Juglans cinerea, Juniperus virginiana, Pinus rigida, Populus balsamifera, Prunus serotina, Quercus bicolor, Q. ellipsoidalis, Sorbus decora, Ulmus thomasii, Picea rubens, P. glauca, P. mariana* and *Abies balsamea.* A number of trees attain their northern limits in Ontario and usually in eastern North America within the region, including *Acer nigrum, A. negundo, Amelanchier arborea, Betula populifolia, Carpinus caroliniana, Carya cordiformis, C. ovata, Celtis occidentalis, Juglans nigra, J. cinerea, Juniperus virginiana, Pinus rigida, Platanus occidentalis, Quercus muehlenbergii, Q. velutina, Salix amgydaloides* and *Ulmus rubra.*

Within this region there is considerable topographic contrast as well as bedrock differentiation and there is much rock outcropping, the latter on and around the Niagara Escarpment particularly as it reaches its northern extent in the Bruce Peninsula and on Manitoulin Island. There is thus much more environmental differentiation and ecological opportunity for vegetational landscapes, systems and communities than in the Deciduous Forests Landscape Region southward. There is less land suitable for agriculture and more natural forests and other vegetation survive in this region.

The influence of coniferous trees is strongly expressed in the dry forests on rock and on sand substrates. The major dominants are *Pinus strobus, P. banksiana, P. resinosa* and *Thuja occidentalis.* The latter species occurs on high, dry, rocky sites but it is also found as a major dominant in wet-mesic and wet so called Cedar Swamps, which are a very characteristic aspect of this landscape region. There are also some boreal conifers which are important on sandplains in the northern areas including *Picea glauca* and *Abies balsamea.* The most frequent associates of *Pinus strobus* in the dry sites are *Pinus resinosa, Quercus rubra, Picea glauca, Betula papyrifera* and *Acer saccharum.* Those trees associated with *Pinus banksiana* as a dominant are *Pinus resinosa, Populus tremuloides, Picea glauca, Thuja occidentalis, Picea rubens* and *Populus grandidentata,* although this pine is often found in solid pure stands which have a very strong impact on the landscape especially when occurring on the summits of rock knolls and mountains. The species growing with *Thuja occidentalis* which is strongly associated with rocky sites and more southward in the region on shallow limestone areas, are *Betula papyrifera, Populus tremuloides, Abies balsamea* and *Picea glauca. Pinus resinosa* is a dominant more frequently northward and on sand and is there associated with *P. strobus, Thuja occidentalis, Pinus banksiana* and *Populus grandidentata.* Another significant dominant in the dry deciduous-evergreen forests is *Quercus rubra* particularly on sand soils and it is much more frequent southward than in the northern granitic areas. It may occur in almost pure stands but is also associated with *Acer saccharum, Betula papyrifera, Pinus strobus, P. resinosa* and *Quercus alba.* Other species which may be dominants in dry forests include *Populus tremuloides, P. grandidentata, Quercus macrocarpa* (which may also form extensive savannas on shallow soils over limestone on Manitoulin Island), *Q. alba, Juniper-*

*us virginiana* (which also forms savannas on sandplains), *Picea glauca, Betula papyrifera, Pinus rigida* (only in the Thousand Islands region on granite) and *Abies balsamea.* There are a number of cliff, talus, rock outcrop and open barrens communities on dry and very dry sites, as well as a number of dry prairies and tall upland dry thickets dominated by *Rhus typhina, R. glabra, Cornus racemosa* and *Prunus virginiana.* Some rock outcrops and dune systems support sand prairies and dune grass communities as well as low thickets dominated by *Juniperus horizontalis, J. communis, Prunus pumila* and *Comptonia peregrina.*

Coniferous trees are important dominants in the dry-mesic Deciduous-evergreen Forests Landscape region particularly on limestone rock and sand substrates in the southern areas and on granite rock and sandy soils in the north. In the southern areas, *Thuja occidentalis* is the most important coniferous tree, whereas *Pinus strobus* and *Abies balsamea* are in the northern areas. An increasing number of boreal conifers are found as dominants in the northern sections including *Abies balsamea, Picea glauca* and *Larix laricina* although the latter is more widespread in moist and wet sites. In the south, *Acer saccharum* is still the most significant dominant in dry-mesic habitats and *Quercus rubra* still persists. *Fagus grandifolia* has greatly reduced dominant status as have many other deciduous trees. *Carya cordiformis, Quercus alba, Ulmus thomasii, Tilia americana, Carya ovata* and *Quercus macrocarpa* are seldom dominants even in the southern parts of the region. Successional deciduous trees which have more northern geographical affinities now are found with greater frequency - *Betula papyrifera* is by far most important in this respect, but *Populus tremuloides* and *P. grandidentata,* also occur. Other trees found uncommonly as dominants but widespread as subdominants include *Fagus grandifolia, Tsuga canadensis, Acer rubrum, Tilia americana, Quercus alba* and *Pinus resinosa.* Cliff communities, sand prairies and occasionally open alvar communities contribute to the landscapes on this moisture regime.

In the mesic deciduous-evergreen forests where conditions are optimum for the development of regional terminal or climax stages, the pattern of dominance is predominantly deciduous and the major dominant is *Acer saccharum.* To a high degree these forests resemble those on mesic sites in the more Southern Deciduous Forests Landscape Region. This convergence under different climatic regimes is a phenomenon worthy of careful investigation. Of 46 sites sampled throughout the southern parts of the region, 33 (72 %) are dominated by *Acer saccharum,* and of 22 in the north, 12 or 55% are so composed. Although *Fagus grandifolia* is present it is not a frequent codominant or subdominant, but *Tilia americana, Tsuga canadensis, Fraxinus americana, Ulmus americana, Betula lutea* and occasionally *Acer nigrum* are the common associates. *Tsuga canadensis* is a dominant on mesic sites in the southern sectors of the region and *Acer saccharum* is the most frequent associate. Although *Tsuga canadensis* is a coniferous tree it is ecologically similar to *Acer saccharum* and other deciduous species. Other deciduous trees occasionally dominating forests on mesic sites are *Quercus rubra, Acer nigrum* and *Ulmus americana.* Northward such trees as *Picea glauca, Abies balsamea, Picea mariana* and *Populus tremuloides,* may be occasional dominants on mesic sites.

Coniferous forest types particularly those dominated by *Thuja occidentalis,* but also *Tsuga canadensis* and *Abies balsamea,* form a prominent position in the wet and wet-mesic forests of the Deciduous-evergreen Forests Landscape Region. These are usually referred to as "Cedar Swamps", and are indeed a very recognizable part of the landscape in moist and wet lowland depressions throughout the region, particularly in the southern areas. These swamps tend to have a stronger participation of boreal coniferous trees particularly in the northern areas. As well, stands may be dominated by these trees including *Abies balsamea, Larix laricina* and *Picea mariana.* More northern boreal-centered deciduous trees such as *Populus tremuloides, Betula papyrifera* and *Populus balsamifera* are also present in these systems and may also dominate successional and burned over areas. A number of other trees should be mentioned for their contributions to dominance and subdominant status in these wet-mesic forests- *Tsuga canadensis, Ulmus americana, Acer rubrum* and *Tilia americana,* the latter two species are strongly represented only in southern areas. Others found as dominants only southward are *Betula populifolia,* a more eastern species, restricted geographically in Ontario, *Quercus bicolor, Acer nigrum, Quercus macrocarpa* and *Fraxinus americana.* Those dominant in the northern areas on wet-mesic sites additionally are *Pinus strobus, Fraxinus nigra* and *Betula lutea. Fraxinus pennsylvanica* dominates stands throughout but is quite restricted. Tall willow thickets may also be a noticeable feature of wet-mesic depressions associated with these cedar swamp systems.

The wet forests in the southern areas of this region occur in both lowland and bottomland topographic sites. The lowland forests are dominated by *Ulmus americana* with *Fraxinus nigra* or *F. pennsylvanica* and *Acer saccharinum* when situated on loams but forests on organic substrates are strongly dominated by *Thuja occidentalis, Larix laricina* and *Picea mariana.* The latter southward are strongly dominated by *Thuja occidentalis,* whereas *Picea mariana* is the strong major species in northern areas. Other dominants in these organic cedar swamps or northern conifer bogs are *Populus balsamifera, Abies balsamea, Betula papyrifera* and *Populus tremuloides.* In the south part of the Deciduous-evergreen Forests Landscape Region, wet forests are found in river bottomland sites and such stands are strongly dominated by *Acer saccharinum, Fraxinus pennsylvanica* and *Salix nigra.* These bottomland sites are very uncommon in the northern areas on the granite bedrock of the Laurentian Shield because the river valleys have been cut very angular and extensive bottomland terraces are infrequently developed.

Associated with these wet forests but in very wet sites are a profusion of more open systems-sedge and grass meadows, fens and tall thicket communities. These are found in increasingly wet habitats on lakeshores, along rivers and in extensive low depressions where drainage is sluggish. The activities of the beaver (*Castor canadensis*) produce massive flooded ponds which destroy the existing vegetation, provide wet environments for these communities to develop, and initiate wetland succession when they migrate to other areas when the food supply (*Populus tremuloides*), has become exhausted. The tall thickets southward are dominated by *Alnus rugosa, Cornus racemosa, Salix rigida, Cornus stolonifera, Rhamnus alnifolia, Salix interior, S. lucida, S. petiolaris, S. bebbiana, S. discolor, Cephalanthus occidentalis* and *Spiraea latifolia,* and by many of the same species as well as *Chamaedaphne calyculata, Myrica gale* and *Nemopanthus mucronata* in the northern areas. Sedge meadows have *Carex aquatilis, C. lasiocarpa* and *C. stricta,* as dominants and *Calamagrostis canadensis* and *Phalaris arundinacea* are most important in the grass meadows. The fens are most frequent in the northern areas and have *Rhynchospora alba, Carex lasiocarpa, Menyanthes trifoliata, Eleocharis rostellata, Scirpus caespitosus, Cladium mariscoides,* and *Myrica gale* as dominants. In saturated conditions marshes dominated by *Scripus acutus, Typha angustifolia, T. latifolia, Phragmites communis, Calamagrostis canadensis, Scripus cyperinus,* as well as other species, are common.

### 3. The Boreal Forests Landscape Region

The landscapes of this extensive region are generally subdued relative to the great expanses of flat terrain involved. These include particularly the Clay Belt Region of north central Ontario which was the bed of a tremendous postglacial lake and also parts of the Hudson Bay Lowlands which cover vast expanses of terrain in an arc surrounding the Bay of the same name. Adjacent to the north shore of Lake Superior there is a mountainous region of very vigorous topography which has considerable influence on the vegetation there.

The vast expanses of flat terrain have only been ice-free for a few thousand years and thus there has been little time for the development of a vigorous drainage network. As a result these flat areas are extremely sluggishly drained and marshes, meadows, wet thickets, bogs and swamp forests are an intergal and significant part of the landscape systems.

Other aspects of the vast boreal region that have a profound affect on the ecology of the landscape components include the catastrophic outbreaks of spruce budworm (*Choristoneura fumiferana*) populations which can leave large tracts of forest denuded and eventually dead, the strong influence of wind which can blow down large tracts of forest, and particularly fire which may reduce forested areas to bare ground and produce an initial stage of succession. A majority of these fires are now known to result from natural causes. One can appreciate the devastating effects of fire when it is coupled with windfall and spruce budworm infestations. An anomalous situation may result from these perturbations because a forest in which the major tree dominants are coniferous is devastated suddenly may become dominated by successional trees which are totally deciduous. Such trees are *Beluta papyrifera, Populus tremuloides* and *P. balsamifera.* These trees often form extensive monodominant or mixed broadleaved deciduous forest which in the subsequent generation may revert strongly or totally to needle-leaved evergreen trees. Another tree which is successional and acts in much the same way, but is coniferous, is *Pinus banksiana.* It in fact has serotinous cones which facilitate reproduction after fires. It can form monodominant forests especially on sandplains or rocky slopes and promontories.

Thus although the forests of the boreal zone are often characterized as coniferous dominated, in point of fact there are deciduous, coniferous as well as mixed coniferous-deciduous types. An additional anomalous type is dominated by *Larix laricina* which is a deciduous coniferous species.

Within the Boreal Forests Landscape Region the tree flora is greatly reduced and includes only 27 species. Of these, 9 are coniferous and 18 deciduous. Of the conifers, 5 are of major importance and occur throughout. They include *Picea mariana, P. glauca, Abies balsamea, Pinus banksiana* and *Larix laricina.* The remaining four are restricted to favourable sites and are only locally important. *Tsuga canadensis* reaches a northern limit in the southern parts, *Pinus strobus* and *P. resinosa* are at northern limits in the central areas and *Thuja occidentalis* is at a northern limit in the northern boreal region. Of the 18 deciduous broadleaved trees, a number rarely attain tree size - *Amelanchier sanguinea, Salix discolor, Sorbus decora, S. americana* and *Alnus rugosa.* A number attain northern limits in the southern boreal region and include *Prunus pensylvanica, Quercus rubra, Q. macrocarpa, Acer saccharum, A. saccharinum, Betula lutea, Fraxinus pennsylvanica* and *Populus grandidentata.* In the central region *Acer rubrum* is at its northern limit. In the northern region *Fraxinus nigra* and *Ulmus americana,* are also at their northern limits. The region is very extensive from south to north, approximately 800 km, so it is not surprising that so many species reach their ultimate northern geographic limits within it. It can be understood also that throughout the region because of successional disturbances at different intervals the landscapes are essentially a matrix of deciduous, coniferous and mixed forests forming extensive natural mosaics. The complexity of these mosaics is related to the physiographic conditions and the variety of tree species, which varies from 28 in the southern parts to 18 in the central areas to as few as 13 in the northern.

The soils, due to the bedrock and type of litter decomposition are decidedly acid and support an extensive acidophyllic flora. Many of the species which occur in the understorey of the evergreen forests are also evergreen, an adaptation to the short growing season and also perhaps the heavy lasting snowfall (Carleton and Maycock, 1978).

Within this region there are abundant granitic knolls with much rock outcropping. These are habitats for a wide variety of cliff, rock barrens and rock outcrop communities. On very dry and dry shallow soils over bedrock there can be stunted forests dominated by *Pinus banksiana* or *Picea mariana.* In the outcrop and cliff systems *Juniperus communis, Vaccinium angustifolium, Amelanchier alnifolium,* and scrubby *Populus tremuloides* and *Betula papyrifera* may be dominant. On very dry sands open barrens may develop after successive fires and *Vaccinium angustifolium, Comptonia peregrina, Alnus crispa* and *Kalmia angustifolia* are predominant. Very occasionally in the extreme northwestern areas of Ontario, open temperate savannas with *Quercus macrocarpa* as the major species may develop on shallow soils over bedrock.

In the southern areas of the Boreal Forests Landscape Region on dry sites, on shallow soils over bedrock or on well drained sands, the dominant trees in the forests are conifers and *Pinus banksiana* is predominant. Such stands are generally post-fire successional and *Picea mariana* and *Pinus resinosa* are frequent co- or subdominants. Other tree species occurring as dominants are *Picea mariana, Pinus resinosa, P. strobus, Populus tremuloides* and rarely *P. grandidentata. Quercus macrocarpa* is a dominant in dry open savannas. In the dry sites of the central regions *Pinus bank-*

*siana* and *Picea mariana* are the primary dominants and *Populus tremuloides, Betula papyrifera* and *Pinus resinosa* also serve as dominants, the latter two trees uncommonly. In the northern region, forest dominants on dry sites are reduced to *Pinus banksiana* and *Picea mariana.*

Forests growing under dry-mesic moisture conditions in the Boreal Forests Landscape Region are somewhat more diverse than those of dry conditions. Sand and clay substrates support the majority of types which have been noted. The major forest dominant is still *Pinus banksiana* and *Picea mariana* and *Populus tremuloides* are the most frequent associates in the southern areas. *Picea mariana, Populus tremuloides* and *Betula papyrifera* are the other dominants of most frequent occurrence whereas *Abies balsamea, Acer rubrum, Pinus resinosa* and *Populus grandidentata,* are dominants of uncommon occurrence in the southern areas. In the central parts of the region *Pinus banksiana, Picea mariana* and *Populus tremuloides* are strong forest dominants and *Abies balsamea* and *Betula papyrifera* also have considerable frequency as dominant trees of the forest communities. In the far northern reaches of the region *Pinus banksiana* and *Betula papyrifera* are frequent dominants whereas *Picea mariana* and *Populus tremuloides* have been recorded less frequently. In the northern areas there is less diversity not only in the patterns of tree dominance but also in those of the understorey elements of the forest ecosystems.

A number of southern trees including *Acer saccharum, Betula lutea, Tsuga canadensis, Acer rubrum* and *Pinus strobus* occur either as dominants, subdominants or associates in the mesic environments of the Boreal Forests Landscape Region, notably in just the southern areas. These environments are favourable for the development of forests dominated by deciduous trees of the boreal region as well, especially *Populus tremuloides* and *Betula papyrifera,* and these trees with *Abies balsamea* are the major dominants. The mesic sites are the optimum environments and have been stipulated as those for the development of the climatic climax which a number of ecologists, Clements (1928), Weaver and Clements (1938), Halliday (1937) and La Roi (1967), have claimed is forests of *Picea glauca-Abies balsamea* (Fig. 6). If such forests do represent a zonal climax, this is an event which rarely occurs, for such forest types are exceedingly uncommon in the landscapes. In over 100 sampled stands and in countless hundreds observed, the combinations of *Abies balsamea-Picea glauca* and *Picea glauca-Abies balsamea* have occurred only on 10 occasions, 9 and 1 respectively. It could be argued that retrogressive processes are so active in these ecosystems and as a result the climax state is seldom attained, but it could be equally strongly argued that instability is such an integral part of the systems that it is not ecologically sensible or realistic to even consider the possibility of a climax state developing. In addition to the dominants mentioned, *Picea mariana* can be a strong leader in the tree sequences in stands, thus being dominant on the uplands as well as the lowlands in this region, as well as *Pinus banksiana, P. strobus, Acer saccharum, A. rubrum* and *Betula lutea,* in the southern areas. In the central areas *Picea mariana* is also a frequent dominant, and *P. glauca, Pinus banksiana, P. strobus* and *Populus balsamifera* are less so. In the northern areas of the region in addition to the typical patterns of tree dominance, *Picea mariana* is quite frequent and *Populus balsamifera, Thuja occidentalis* and *Picea glauca,* have been so recorded but infrequently. The first occurrence of subarctic forests is found in the northern areas on organic substrates with mesic moisture but become a very recognizable feature of the landscapes on organic and clay substrates particularly under normal and colder microclimatic regimes but on wet-mesic and wet sites.

**Fig. 6.** Old growth virgin mesic upland boreal forest dominated by *Abies balsamea* and *Picea glauca* growing on sandy morainal till. Stout Lake, District of Kenora, northwestern Ontario.

In the wet-mesic forests the dominance of coniferous trees is readily apparent particularly that of *Picea mariana* although *Abies balsamea, Picea glauca,* and *Pinus banksiana* are much less important. *Thuja occidentalis,* although approaching its northern limit here is also found as a forest dominant, but decreasingly so, passing from south to north in the region. Other deciduous species near northern limits also dominate in specialized situations, warmer than normal alluvial sites in the river valleys as well as on moist loam-like soils. These include *Betula lutea,* only in the south, and *Fraxinus nigra* and *Ulmus americana,* throughout. Other species occurring much less frequently as dominants are *Populus tremuloides, Betula papyrifera* and *Populus balsamifera.* In colder than normal wet mesic sites in depressions on organic substrates, open-grown subarctic forests dominated by *Picea mariana,* occasionally with *Larix laricina* are found, as well as oligotrophic conifer bogs, also dominated by *Picea mariana.*

In the wet forests of this landscape region the patterns of dominance are largely dependent on location. In the southern areas on loam soils southern deciduous outliers, *Fraxinus nigra* and *Ulmus americana* grow on rich valley alluvium. On clay, dominance is divided between coniferous and broadleaved deciduous trees - *Picea mariana, Abies balsamea, Populus balsamifera, Fraxinus nigra, Acer saccharinum, Fraxinus pennsylvanica* and *Ulmus americana.* On organic substrates lowland coniferous bog forests of *Picea mariana, Thuja occidentalis, Abies balsamea* and *Larix laricina* prevail. Unusual forests in lowland bog situations dominated by *Pinus banksiana* are a rare occurrence here. In colder than normal microclimates there are subarctic forests of *Larix laricina* and *Picea mariana,* much farther south than their normal area of distribution.

On wet sites in the central parts of the region, especially on organic substrates, *Picea mariana* is by far the most important dominant and *Larix laricina* is only occasionally a leading species. *Abies balsamea, Thuja occidentalis, Picea glauca* and *Pinus banksiana* are tree species which are closely assocated with these dominants in these environments.

On wet sites in the northern Boreal Forests Landscape Region forest development is mainly restricted to organic substrates and *Picea mariana* is the major dominant although *Larix laricina* may also fulfill this role or be a co-dominant or subdominant. On wet clays *Picea mariana, Larix laricina* and *Populus balsamifera* are dominant. In outlying subarctic forests on organic and occasionally clay soils, *Picea mariana* and *P. glauca* with or without *Larix laricina* are the major forest formers. Tall lowland thickets are also a prominent landscape feature often found on the fringes of the wet lowland forests occupying great expanses of terrain. A number of shrubs are widespread in these thickets including *Salix discolor, Alnus rugosa, A. crispa, Betula pumila, Salix interior, Cornus stolonifera, Salix planifolia, S. rigida, S. petiolaris* and *Chamaedaphne calyculata.* Sedge and grass meadows and occasionally southern wet tundra outliers may be found adjacent to these open and semi-open communities.

Throughout this region there are extensive flatlands and thus drainage is poor. In these broad basins wetlands have developed and depending largely on water depth as well as movement, very different types of systems develop including thickets and swales, grass meadows, sedge meadows, fens, marshes and various aquatic communities. When occupying considerable areas these communities may have a very visible effect on the landscapes. Within the scope of this contribution, it is impossible to deal with all of these diverse systems in detail, but they are so widespread in this region that it is worth mentioning some of them. A number of the dominants of these communities occur throughout the extensive boreal region, others are restricted to various sectors. As an example, saltwater systems are restricted to the northern areas along the coast of James Bay and only there can saltmarshes, saltpan and other salt-influenced communities be found. Such systems are dominated by *Hippuris vulgaris, Salicornia europaea, Scirpus maritimus, Eleocharis halophila, Carex paleacea, Puccinellia phryganodes, Senecio congestus* and a number of other salt-tolerant species.

In very wet conditions tall thickets dominated by *Alnus rugosa, Betula pumila, Salix interior, S. discolor* or *S. bebbiana* and low thickets by *Myrica gale, Salix pedicellaris* or *Chamaedaphne calyculata,* occur throughout the region. In the northern areas other shrubs including *Betula glandulosa, Salix planifolia, S. serissima, S. glauca* and

*S. candida* may form thickets. Sedge meadows dominated by *Carex lasiocarpa, C. aquatilis, C. rostrata* and *C. lacustris* may be found through the region whereas *Carex stricta* may be a major species only southward, *C. oligosperma* centrally and *C. vesicaria* only northward. Under similar conditions meadows develop under the dominance of *Calamagrostis canadensis* which may be found alone or with various species of sedge. These occur throughout the region but are more prevalent southward. Under saturated conditions, water levels several centimeters above substrate are maintained throughout the growing season but may also fluctuate considerably. In these conditions, marshes formed by a number of emergent species, are common. *Typha latifolia, Scripus validus, Carex lasiocarpa, Sparganium americanum, Equisetum fluviatile, Eleocharis palustris, Carex aquatilis* and *Phragmites communis* are found throughout the region as major dominants in these systems. In open water situations on lakeshores and wide areas of rivers in calm, less exposed locations, many different aquatic communities develop. *Nuphar variegatum* and *Sparganium angustifolium,* are components of floating communities throughout whereas *Nymphaea odorata* is found southward and *Sparganium fluitans, Polygonum amphibium* and *Nuphar microphyllum* northward. In submerged communities there are many members of the genus *Potamogeton, P. filiformis, P. zosteriformis, P. richardsonii, P. pectinatus, P. gramineus* and *P. natans* as well as *Sagittaria cuneata, Eleocharis acicularis, Utricularia vulgaris, Myriophyllum exalbescens,* etc.

### 4. The Boreal Subarctic Forests Landscapes

Proceeding northward the conditions for forest growth progressively deteriorate until trees approach the ultimate endurance of extreme low temperatures and a brief growing season. These limiting conditions are first expressed in a decrease in stature but eventually the trees become widely separated and as a result open-grown, and produce a forest system which in many aspects resembles a savanna. These systems could be rightfully described as boreal savannas. The same phenomenon occurs at higher altitudes but in this central region of Canada high elevation outcropping rock promontories are not present.

**Fig. 7.** Mesic open-grown valley forest dominated by *Picea glauca* in the Subarctic Forest Region, north of Knob Lake in central Labrador, eastern Canada, typical of that in the central regions of northern Ontario.

Drainage conditions strongly influence the development of vegetation. Often series of old raised beaches occur parallel to the seashores but well inland. These are ancient shorelines which have been formed by the gradual uplift of the land since the recession of the glaciers. These old shorelines permit drainage and thus the development of forests, subarctic or boreal. The moist to wet intervening lowlands and the more recently freed coastal areas which are very young successionally, are only suitable for the development of open tundra systems. Any higher land which is exposed to the severe winds also supports dry depauperate tundra communities. Thus the landscapes of the region are extremely complex and are mosaics of relatively dense but very restricted boreal forest, extensive open-grown subarctic forests with widely spaced trees either lichen woodlands or moist mossy woodlands, interspersed with dry upland tundra or wet lowland tundra. As well sedge and grass meadows, open bogs, fens, and low willow thickets and marshes of low-statured rushes and horsetails are common and may occupy vast stretches of the landscape.

The ecosystems formed of widely spaced open-grown trees and growing over slightly undulating terrain, form one of the most scenic and majestic landscape regions of Canada and the world (Fig. 7). They are particularly attractive in the winter condition.

The open grown condition permits many shrubs to become established in the forest understorey. Despite the reduced number of trees, now only six, four conifers and two deciduous, they are still sorted out on the terrain in terms of the moisture features of site. There are thus still dry, dry-mesic, mesic, wet-mesic and wet forests, and although these trees have much broader tolerance than species farther south, these moisture regimes are dominated by different species combinations. The open-grown aspect permits much light to reach the forest floor and in dry to mesic substrates the major ground cover is lichens and in mesic to wet, mosses predominate. From the air the views of widely spaced trees with grey to light brown lichen ground cover on dry sites, with yellow to green on mesic areas and green floors in wet sites, are quite spectacular.

The trees remaining include *Picea mariana, P. glauca, Larix laricina* and very occasionally *Pinus banksiana.* In rich river flood plains *Populus balsamifera* can still form monodominant deciduous forests and many southern understorey species extend much farther north in these favourable habitats. The other tree species is *Populus tremuloides* which is rarely found in drier environments but more freguently on better loam soils. Despite the small numbers of species, a variety of forest communities occurs on the various environments available. The majority of forest communities are dominated by coniferous trees but some mixed coniferous-deciduous types do occur.

Unusual conditions prevail in respect to the occurrences of forests in this region. It gives the impression physiognomically that it comes under the influence of a climatic regime which is favourable for forest development, but on the contrary, it is decidedly limiting for forests. Almost no forest communities are formed in sites which have colder than normal microclimate, with the exception of wet-mesic and wet sites on organic substrates. In some cases such sites are on raised palsa mounds pushed up by frost action, and this provides drainage and perhaps increased possibility for aeration. There are increased ecological opportunities for subarctic forests on sites with normal microclimates on moister sand and on organic substrates with mesic, wet-mesic and wet conditions. The greatest opportunities for the development of forest communities in the region are in warmer than normal microclimates but on soils with better drainage capabilities particularly sands loams and clays with dry-mesic and mesic moisture characteristics. On warmer than normal sites in the mesic, boreal rather than subarctic forests are found. On organic substrates forests of a boreal rather than subarctic character are found only on wet warmer than normal sites.

This poses a question as to what grows under the other site conditions which exist here, if subarctic or boreal forests do not. Since such sites are beyond the environmental limits of forests, the natural sequences of vegetation are of course subarctic tundra. Under colder than normal conditions a great variety of tundra communities are found including maritime strand tundra, heath tundra, carpet tundra, palsa tundra, solifluction tundra, marsh tundra, etc. Thus tundra vegetation occurs quite far south of the region where it forms the major plant cover by taking full advantage of those microclimatic situations which are totally impossible for the growth of forests.

In this region generally there is a restriction in the ecological opportunities afforded for the development of natural vegetation. A variety of soils as well as good soils are lacking, and there is relatively little topographic variation. Thus restricted microclimatic variation, and the advent of permafrost, solifluction activities, and a very reduced growing period, have essentially constricted the environmental gradients available. Thus if arid or very dry environments occur here, no vegetation has been found growing in them and relatively few communities have been recorded even in dry habitats. A few granite cliff and talus communities occur on the dry sites with grasses and low shrubs and herbs as occupants. Subarctic forests on rock are dominated almost exclusively by *Picea mariana* and are restricted to warmer than normal sites under dry conditions.

In colder than normal dry-mesic sites, raised beach tundra with *Salix glauca* or *Hedysarum mackenzii* is frequent, mat tundra with *Dryas integrifolia* and *Empetrum nigrum* and heath tundra with *Juniperus communis* is present, as well as coastal dune thickets dominated by *Shepherdia canadensis* and *Salix glauca.* On sand in normal microclimates, river flat tundra with *Salix calcicola* and *S. glauca* and krummholz of *Picea glauca* occurs. In warmer dry-mesic sites subarctic forests mainly with *Picea mariana* and boreal forests of *Picea mariana* and *Pinus banksiana* or *Populus tremuloides* with *Picea mariana,* have extended beyond their normal geographic range.

Mat tundra with *Dryas integrifolia* as major species and heath tundra dominated by *Rhododendron lapponicum* and *Salix reticulata* are present in colder than normal mesic situations. Although heath tundra with *Equisetum scirpoides* and *Rhododendron lapponicum* occurs in normal mesic sites, the predominant vegetation is subarctic or boreal forests with *Picea mariana* systems on organic peats and *Picea glauca* and *Larix laricina* on sand. In mesic warmer environments boreal deciduous forests dominated entirely by *Populus balsamifera* grow along the terraces of the rivers flowing into James Bay. Subarctic forests composed mainly of *Picea mariana* on mesic sands and of *Picea mariana* or *Picea glauca*, the latter in coastal situations, but both on mesic clays and in warmer locations, are common.

The wet-mesic and wet environments under all microclimatic situations are much more productive of forests than the other moisture regimes of the Subarctic Forests Landscape Region. In wet-mesic colder sites tundra communities are widespread and subarctic forests dominated by *Picea mariana* with or without *Larix laricina* are the only types and are found only on peats underlain by permafrost. The tundra communities include open sparse rock tundra, with *Anemone parviflora* and *Astragalus alpinus*, moist meadow tundra with *Deschampsia cespitosa* and *Juncus arcticus*, moist tundra with *Equisetum arvense* and *Salix reticulata*, solifluction heath tundra with *Salix reticulata* and *Vaccinium uliginosum*, and palsa tundra dominated by *Rubus chamaemorus* and *Vaccinium vitis-idaea*. In wet-mesic normal microclimates, subarctic forests dominated by *Picea mariana*, occasionally with *Larix laricina* are found growing on clay and organic soils. Low shrub tundra with *Salix planifolia* and *Betula glandulosa* and lowland thickets of *Alnus crispa* are on rock whereas river flat tundra of *Equisetum arvense* and tundra meadows with *Equisetum variegatum* and *Carex aquatilis* are frequent on clays. In warmer wet-mesic coastal areas on clay, subarctic coastal forest dominated by *Picea glauca* is common and tall lowland thickets of *Salix planifolia* are a feature of sandplains.

In wet environments of the Subarctic Forests Landscape Region, forests either subarctic or boreal, occur mainly on organic substrates. The latter are found only on such substrates and under warmer microclimates and may be dominated by *Picea mariana, P. glauca* and *Larix laricina* but often the latter occurs as an associate species. Under normal microclimates on organic soils, subarctic forests are dominated by *Picea mariana* with *Larix laricina* and subarctic thicket fens which are very extensive in the coastal areas are dominated by *Larix laricina.* On clay, subarctic coastal forests of *Picea glauca* and *Larix laricina* are common and low shrub tundra dominated by *Salix candida* with *S. planifolia* and *S. glauca* also occur. Sedge meadow tundra with *Equisetum variegatum* and *Carex aquatilis* is found also on organic soils. In colder microclimatic conditions on organic substrates subarctic forests of *Picea mariana* and *Larix laricina* occur with *Scirpus hudsonianus* fen and heath tundra of *Salix reticulata* and *Vaccinium uliginosum.* On wet clay and loam soils several tundra communities, seepage tundra with *Carex microglochin* and *Juncus filiformis,* solifluction tundra with *Equisetum variegatum* and *Saxifraga aizoides,* and marsh tundra dominated by *Carex aquatilis,* are frequent.

Under very wet conditions in this region a variety of sedge meadows dominated by *Carex aquatilis* or *C. rostrata,* grass meadows with *Deschampsia cespitosa, Calamagrostis neglecta* and *Puccinellia phryganodes,* the latter in brackish sites, fens with *Scripus hudsonianus, S. cespitosus, Eleocharis pauciflora* or *Carex aquatilis* and low-statured lowland thickets dominated by *Salix planifolia, S. candida, S. glauca, Myrica gale* or *Betula glandulosa,* occur mostly on organic or clay soils. Tundra communities begin to merge with sedge or grass meadows, fens and thickets and the floras of these systems which are found southward become mingled with those which are more prevalent in arctic regions. Thus what was considered a sedge meadow in more southern landscape regions is described as wet sedge tundra here and also in the Subarctic Tundra Landscape Region.

Under saturated moisture conditions on clay or organic soils, marshes but of low stature are found dominated by *Hippuris vulgaris, Carex limosa* and *Menyanthes trifoliata, Eleocharis pauciflorus, E. palustris, E. uniglumis,* the latter in tidal areas, *Equisetum fluviatile* and *Carex aquatilis.* Occasionally open bogs of *Scheuchzeria palustris* and scattered shrubs occur.

Finally in open water, submerged, floating and emergent aquatic communities abound, particularly in water bodies with clay or organic bottoms. These include submerged types dominated by *Myriophyllum exalbescens, Ranunculus subrigidus, Potamogeton richardsonii, P. filiformis,* or *Ranunculus trichophyllus,* floating dominated by *Nuphar variegatum* or *Glyceria fernaldii* and emergent communities with *Hippuris vulgaris* and *Sparganium angustifolium.*

## 5. The Subarctic Tundra Landscape Region

The extended shores of Hudson and James Bays are essentially treeless (Fig 8). The ice-covered bays, in such condition both in the prolonged winter season and in the brief summer due to pack ice, do not ameliorate the climates of the adjacent coastal areas, but in fact intensify the colder regimes. Trees can only survive in the warmer river valleys and on well-drained former beach ridges, but the predominant vegetation is essentially tundra. Another factor of great significance is that much of the area is underlain by permafrost and the depth of the active layer has a decisive effect not only on the lack of tree growth, but also the establishment of many plants typical of the tundra. These communities differ in only minor respects from tundra systems farther north. In areas where snow may accumulate, and usually there is sparse snow cover, it is possible for certain shrubs to grow to about a meter in height. The snow protects these willow and dwarf birch shrubs from winds, blowing snow, and ice crystals which simply shear off living plants. Another feature is that due to more favourable moisture generally as well as comparatively and less severe climatic and environmental conditions than those prevailing farther north, a much higher ground cover develops in subarctic tundra communities, and a comparatively large number of shrubs, many prostrate, contribute to the vegetation. Thus the subarctic tundra appears well vegetated. The plants are low and depauperate but they project extensive cover and much of the ground surface between the vascular shrubs and herbs except in severely limiting conditions, is covered with either lichens or mosses or both.

**Fig.** 8. Old raised beaches on the Belcher Islands. southeast Hudson Bay with different tundra ecosystems on the various old beach shorelines resulting from the drop in sea levels following deglaciation.

The only situations where forest, and only subarctic forest, has been found is on wet-mesic clay soils, growing under warmer microclimatic conditions on old raised beaches, and well inland. Tall lowland *Salix planifolia* thickets and subarctic thicket fens of either *Larix laricina* or *Picea mariana* are restricted to wet organic substrates, again in warmer sites.

Thus the landscapes of this coastal fringe region are composed of low depauperate tundra with occasional patches of shrub tundra fringing the river systems and restricted inclusions of subarctic forests on old beach lines in more inland areas. These systems form a very astonishing contrast to the great variety of forested ecosystems which are the major elements in the landscape regions to the south.

In dry conditions exceedingly sparse vegetation is found. On rocky or sandy coastal beaches or strands, communities dominated by *Elymus arenarius* with *Festuca rubra, Arenaria peploides* and *Potentilla pulchella* develop.

Under dry-mesic site moisture particularly in normal and colder than normal microclimates, the tundra communities are composed of a number of woody prostrate shrubs and heaths which include willow scrub with *Salix hudsoniensis, S. calcicola,* or *S. glauca* as dominants, lichen heath dominated by *Empetrum nigrum, Dryas integrifolia* or *Ledum decumbens,* grass heath and beach systems with *Elymus arenarius* or *Poa alpigena.* Some examples of lichen heath tundra have well developed polygons, particularly in colder than normal situations, providing evidence of the frost action which is prevalent throughout the region and attests to the severe and limiting climate.

Mesic moisture conditions provide the greatest ecological opportunities for the development of communities in the region and on the largest variety of substrates and microclimatic situations. In colder than normal sites, old raised beach heath, lichen heath polygon tundra on sand, and willow-heath tundra on clay, are dominated by *Empetrum nigrum, Dryas integrifolia* and *Salix reticulata* respectively. Under normal microclimate on sand, old raised beach tundra with *Dryas integrifolia,* lichen polygon tundra with *Empetrum nigrum,* heath mat tundra with the same species and low shrub tundra with *Salix glauca,* are present. As well, on clay, upland heath tundra with *Dryas integrifolia* and *Vaccinium uliginosum* as well as shore grass meadows dominated by *Festuca rubra* and *Salix brachycarpa* contribute to the vegetation cover. Although certain plant species are dominant in a variety of communities because of wide ecological tolerances, associates differ depending on the specific environmental conditions and provide an expression of the variation in environments. In normal mesic sites on accumulated organic debris on the upper tidal drift lines which extend for great distances because the topographic variation is so slight, salt tolerant species like *Matricaria inodora* and *Chrysanthemum arcticum* predominate and are associated with *Rumux maritimus, Festuca rubra, Puccinellia phryganodes, Potentilla egedii* and *Senecio congestus.* Under warmer mesic conditions low shrub tundra dominated by *Betula glandulosa, Salix brachycarpa, S. hudsoniensis* or *S. glauca* are found on sands and clays.

A variety of tundra communities are recorded for colder and normal wet-mesic sites. Solifluction mound tundra is dominated by *Ledum decumbens* and *Vaccinium vitis-idaea* and wet depression tundra by *Scirpus cespitosus* and *Salix calcicola* and both occur on sand. On clays under normal microclimates a number of different salt tolerant tundra communities are located adjacent to the shore. These include shore flat meadows, shingle slope and salt meadows, all dominated by *Puccinellia phryganodes* with combinations of other species, and drift line vegetation with *Senecio congestus* as a major species. Fresh water systems are grass meadows with *Poa arctica* and *Calamagrostis neglecta,* and low shrub tundra dominated by *Festuca rubra* and *Salix hudsonensis* or *Salix calcicola* and *S. planifolia.* In warmer conditions a variety of tall thickets are found on sand or clay with *Salix planifolia* or *S. glauca* as major species. Grass meadows on clay with *Poa alpigena* and *Petasites sagittatus* are common. Warmer than normal clay soils on wet-mesic sites on old beach ridges are the only suitable environments for the development of *Picea mariana* dominated subarctic forests the most northern forest outliers in the region of central Canada.

In wet brackish environments adjacent to coastal areas extensive meadows dominated by *Puccinellia phryganodes* with *Potentilla egedii, Stellaria humifusa* and *Rununculus cymbalaria* exist and these are prime feeding grounds for the vast flocks of geese in the region. On wet organic sites under normal conditions, meadows of *Equisetum arvense* are present but in warmer environments, tall lowland thickets dominated by *Salix planifolia* and *S. candida* thrive. Subarctic thicket fens, communities with widely spaced short-statured depauperate *Larix laricina* or *Picea mariana,* form extensive systems. On warmer than normal clay sites sedge meadows with *Carex aquatilis* and *Poa arctica* find suitable conditions.

The very wet habitats with organic substrates are favourable for calcareous fens with *Carex limosa, C. livida, Scirpus cespitosus* and *Eriophorum angustifolium* or for sedge-horsetail marshes dominated by *Carex aquatilis* and *Equisetum fluviatile.* Near the coast in saline, very wet depressions, communities dominated by *Hippuris vulgaris, Rumex maritimus* and *Senecio congestus* occur as widely scattered dark green potholes over the extensive expanses of flat clay plains.

In saturated environments a series of marsh communities are frequently observed in which *Hippuris vulgaris, Menyanthes trifoliata* or *Carex aquatilis* are dominant depending on the condition of the water - saline or calcareous. Some submerged communities dominated by *Ranunculus trichophyllus* are found in shallow waters.

Finally in open water a variety of different submerged aquatic systems are found. There seem to be few if any floating aquatics which have been able to persist in the harsh climates of this region. *Potamogeton filiformis, Ranunculus trichophyllus, R. aquatilis* and *Myriophylum exalbescens* are dominant in the submerged communities.

### Concluding Remarks

These five major landscape regions which involve ten vegetational and floristic regions - southern deciduous forests, temperate savannas, tallgrass prairies, southern and northern deciduous-evergreen forests, southern, central and northern boreal forests, subarctic forests and subarctic tundra, occur over 15 degrees of latitude or 1600 km of terrain in central Canada. This vast extent of territory includes about 4500 vascular plants. By way of contrast the Japanese Archipelago excluding the outlying Southern Ryukyu and Okinawan Islands, also extends over 15 degrees of latitude and involves major vegetational regions-broadleaved evergreen forests, deciduous forests, evergreen - deciduous forests, boreal forests, subalpine forests and alpine tundra. There is probably more altitudinal than latitudinal variation in the many unusual ecosystems found here. These islands have a flora of perhaps 6500 species. The sequences of vegetational systems in the two regions are remarkably similar.

The broad-leaved evergreen warm temperate forests of Japan find no counterpart in central Canada just as the subarctic forests, clearly severe boreal temperate, find no comparable systems in Japan, although the subalpine tundra and subarctic tundra have much in common. As well, in Japan there are no tallgrass prairies or temperate savannas although these communities are outliers at their northwestern limit in southern Ontario and are decidedly limited.

There are great similarities between the floras of these regions. Many families and genera and even some species are common. Many genera and species are very closely related taxonomically and ecologically. Almost all of the tree genera found in central Canada with the exception of *Carya, Liriodendron, Nyssa, Platanus, Gymnocladus* and *Sassafras* are also found in Japan. All of these genera in Canada are represented by only a single species of tree, and these are seldom dominants in the forests. The exception is *Carya* which has 6 representatives, two of which, *C. ovata* and *C. cordiformis* may dominate stands. Many tree genera are common to Ontario and Japan- *Abies, Juniperus, Larix, Picea, Pinus, Taxus, Thuja,* and *Tsuga* of the conifers, and *Acer, Aesculus, Alnus, Amelanchier, Betula, Carpinus, Castanea, Celtis, Cornus, Crataegus, Prunus, Quercus, Rhus, Salix, Sorbus, Pyrus, Tilia* and *Ulmus,* of the flowering plants. A significant group of genera of the ecosystems found in Ontario, grow in the same or similar systems but only in Japan. These include *Acanthopanax, Aphananthe, Aralia* (woody), *Cephalotaxus, Cercidophyllum, Cryptomeria, Kalopanax, Maackia, Phellodendron, Platycarya, Pterocarya, Styrax, Symplocos, Syringa, Thujopsis, Torreya* and *Zelkova,* and attest to the much richer flora of Japan. As well, many genera of shrubs and herbs in these associated ecosystems are found in both regions but there are many additions in Japan.

Although many genera occur in common between these widely separated localities, many of the species within these genera are not necessarily ecological counterparts. On a taxonomic basis, many species are considered to be ecological vicariads, as for example *Ostrya virginiana* and *O. japonica.* In fact these species do not occupy the same ecological situations, the North American member being predominantly a tree of the intrusive or lower canopy layer of the deciduous and southern deciduous-evergreen forests, whereas the Japanese member, becomes a tall tree of the upper canopy in the same ecosystems. *Ostrya virginiana* can be very important in dry-mesic and mesic deciduous forests in Ontario, but *Ostrya japonica* is seldom a significant dominant in Japanese systems. If one compares the performances of understorey herbs, *Maianthemum canadensis,* as an example, is tolerant of a broad range of moisture and soil conditions and is an aggresive member of deciduous, deciduous-evergreen, boreal and even subarctic forests and is also found in many minor vegetational communities, but *Maianthemum dilatatum* is much more restricted environmentally and vegetationally in Japan. If one compares the ecological performances of *Rhus ambigua* and *Rhus radicans,* both woody lianas and often forest flora creepers in deciduous and deciduous-evergreen forests in both Ontario and Japan, it is clear that they are very comparable ecological vicariads. There is a great need to compare similar ecosystems throughout the world but in a more exact way than has been done to this time. They need to be compared quantitatively rather than just descriptively and then there must be a firm quantitative basis for not only comparing ecosystems but also for examining critically the ecological performances and amplitudes of constituent species. At a period when natural systems everywhere in the world are coming under tremendous environmental pressures related to pollution, global climatic change and the results of many increasing human activities, it is critical that this quantitative evaluation take place on a global scale.

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# Preserved Life Orientations of Soft-Bottom Infaunal Bivalves: Documentation of Some Quaternary Forms from Chiba, Japan

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**Abstract** Life orientations of 19 species of soft-bottom infaunal bivalves preserved in the Quaternary of Chiba, Japan, are described, and some are compared to the observation of living specimens. New ecological information was given to bivalves including deep-burrowing lucinaceans and a periplomatid which were ecologically little known. The orientations preserved in the strata agree with the normal feeding orientations in most cases. There are, however, a few examples showing hydrodynamically unstable orientations which are also different from the normal life orientation.

Most of the bivalves described are deep burrowers or those living in protected environment, where water agitation is limited and muddy substrata dominate. This indicates that depths of shell burial and depths of physical disturbance, such as sea-bottom erosion, are the most important factors determining preservation of the bivalve life position. Bioturbation may have played some role in changing the orientation of dead bivalves from the original life position especially in the case of small bivalves. Compaction effect may also have modified the original orientation, increasing the inclination of elongated forms.

**Key words:** life orientation, bivalve, taphonomy, Quaternary.

Recognition of preserved life positions of fossils has long been a common practice for geologists when they are engaged in paleoenvironmental reconstructions, because they are the only definite evidence showing *in situ* burial. Also, an analysis of bivalve life orientations preserved in shell beds has been shown to be a practical tool in interpreting depositional and erosional processes of shell beds (Kondo, 1987a; 1989). Observation of presreved life position is thus important for taphonomists and paleoecologists. In addition, position of benthos within the substratum is considered a clear expression of its ecological adaptation to the physical environment (Stanley, 1970). The description of preserved life positions of ecologically little-known living species would contribute to understanding their life habits, which are difficult to observe for the living specimens in nature.

Descriptions of preserved position of fossil benthos in the strata therefore, are a reliable source of information on which future studies can be based. Precise descriptions of preserved bivalve life positions are, however, very scarce, except for the descriptions of Jurassic bivalves by Fürsich (1980) and occasional descriptions in some paleontology textbooks (*e.g.,* Chinzei, 1973).

This paper deals with the first systematic description of the orientations of the infaunal bivalves preserved in the Quaternary, distributed in Chiba, Central Japan. Also, I will discuss taphonomic and paleoecologic implications of the preserved life positions of the bivalves.

## Life Position of Soft-Bottom Infaunal Bivalves

Each species of soft-bottom infaunal bivalves can assume different positions within the substrata according to different needs in life. Figure 1 shows various orientations assumed by a common Japanese bivalve, *Ruditapes philippinarum* (Adams et Reeve), based on my observation of the living forms on the sand flats in Chiba: a physically stable orientation on being exposed on the sea-botttom (A), an orientation in reburrowing (B; "erect probing orientation", Stanley, 1970), an orientation in the course of burrowing (C), a feeding orientation (D; normal feeding position), and an orientation in escaping on anastrophic burial (E; "inverted erect probing orientation", Krantz, 1974). All these orientations have a chance of being preserved in the stata.

Life position is, in general, defined as the normal feeding position (Stanley, 1970). It is thus important to consider the siphon disposition in determining the life position of a bivalve species. Many examples of bivalve life position can be best understood as the easiest way of positioning

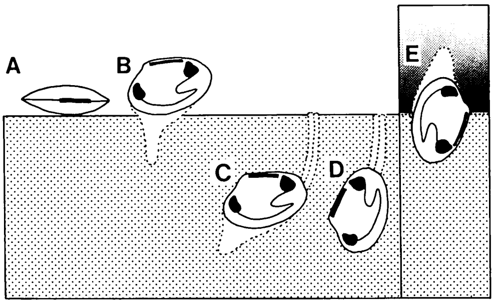

**Fig. 1.** Schematic representation of various orientations assumed by a soft-bottom infaunal bivalve *Ruditapes philippinarum* in life. For explanation, see text.

their siphons or corresponding organs for feeding, as discussed and illustrated by Stanley (1970: fig. 34).

## Field Observation

Shell orientations of conjoined bivalve specimens were measured for 19 bivalve species (Table 1) at the ten outcrops in Chiba Prefecture (Table 2).

Bivalve life position includes depth of shell burial and shell orientation as defined by Stanley (1970). Depth of shell burial cannot, however, be readily observed in the fossil record, and was not inferred in this study. Shell orientation is expressed as the inclination of the commissure plane of conjoined bivalves to the bedding, and the inclination of the long axis, or antero-posterior axis, of the shell to the bedding. In some example, the inclination of the long axis will also be expressed as an angle between the long axis and the vertical from the bedding. These two parameters were used for measurements. Azimuthal orientation was not measured. In the following descriptions, an adjective "vertical" will be used as implying

**Table 1.** List of bivalve species for which life position is documented in this paper.

*Solemya tokunagai* Yokoyama
*Conchocelle bisecta* (Conrad)
*Lucinoma annulata* (Reeve)
*Lucinoma aokii* Hirayama
*Anodontia sternsiana* Oyama
*Clinocardium braunsi* (Tokunaga)
*Saxidomus purpuratus* (Sowerby)
*Callithaca adamsi* (Reeve)
*Callista chinensis* (Holten)
*Paphia undulata* (Born)
*Dosinella penicillata* (Reeve)
*Dosinorbis japonicus* (Reeve)
*Clementia papyracea* (Gray)
*Raeta pellicula* (Reeve)
*Tresus keenae* (Kuroda et Habe)
*Solen krusensterni* Schrekck
*Panopea japonica* A. Adams
*Mya arenaria oonogai* Makiyama
*Periploma otohimeae* Habe

**Table 2.** Observation sites for preserved life position of bivalves.

| locality (all in Chiba Prefecture) | age | sediment | described species |
|---|---|---|---|
| Taitozaki, Misaki-machi: the same locality of O'Hara (1974) | Holocene | mud | *Mya arenaria, Anodontia stearnsiana* |
| Kinu, Futtsu-shi, | Holocene | pebbly mud | *Paphia undulata, Dosinella penicillata* |
| Sakurai, Kisarazu-shi: Loc. 1 of O'Hara et al. (1976) | Late Pleistocene Kioroshi Fm | pebbly mud | *Dosinella penicillata, Panopea japonica* |
| Otake, Immba-mura | Late Pleistocene Kioroshi Fm | very fine sand | *Panopea japonica,* |
| Yoshitaka, Immba-mura | Late Pleistocene Kioroshi Fm | very fine sand | *Panopea japonica, Raeta pellicula* |
| Tsurumaki, Immba-mura | Late Pleistocene Kioroshi Fm | very fine sand | *Raeta pellicula* |
| Nagayoshi, Sodegaura-machi: Loc. 21 of Tokuhashi & Endo (1984) | Middle Pleistocene Kiyokawa Formation | pebbly sand | *Panopea japonica, Tresus keenae, Saxidomus purpuratus, Dosinorbis japonicus, Lucinoma annulata, Callista chinensis, Clementia papyracea, Clinocardium braunsi* |
| Mariyatsu, Kisarazu-shi: Loc. 55 of Tokuhashi & Endo (1984) | Middle Pleistocene Yabu Fm | very fine sand | *Panopea japonica, Tresus keenae* |
| Dai, Kimitsu-shi: 400m NE from Loc. 48 of Tokuhashi & Endo (1984) | Middle Pleistocene Jizodo Fm | sandy mud | *Saxidumus purpuratus, Callithaca adamsi* |
| Tabi, Ichihara-shi: close to Loc. 137 of Tokuhashi & Endo (1984) | Middle Pleistocene Kasamori Formation | silt | *Periploma otohimeae* |
| Kawayatsu, Kimitsu-shi | Middle Pleistocene Kakinokidai Formation | silty sand | *Solemya tokunagai, Lucinoma aokii, Conchocele bisecta* |

the commissure plane is oriented vertically to the bedding.

## Results

Preserved life orientations are described in the following section for each species. Information of the life orientation of the living individuals of the identical species is given for comparative purpose.

### *Solemya tokunagai* Yokoyama

*Life habit.* This species has a large cylindrical shell, more than 10cm long. Living specimens are found in muddy substrata of the upper bathyal zone in the northwestern Pacific (Habe and Ito, 1965). The life orientation of this species has not been described. Stanley (1970) reported that *Solemya velum* Say, a much smaller species than *S. tokunagai,* makes a Y-shaped burrow and stays in the lowest portion of the U-shaped segment of the burrow. There are, however, no workers observed such burrows for other *Solemya* species (Yonge, 1939; Owen, 1961).

*Mode of fossil occurrence.* Seven specimens were observed and measured in the silty sand of the middle Pleistocene Kakinokidai Formation at Kawayatsu (Table 2). The shell orientation is a vertical, anterior up orientation, with the long axis 20° to 35° from the bedding. This is one of the rare examples of an orientation with the anterior portion upward. The smallest individual was found vertical, with the long axis horizontal, and one of the adult individuals was oriented vertically, with the long axis perpendicular to the bedding.

It is uncertain whether *S. tokunagai* was living in a burrow, like *S. velum.* There are no burrow-like structures observed around the *in-situ S. tokunagai* specimens. The inclined long axis of the shell does not seem to be consistent with the orientation within the U-shaped segment of the burrow as observed by Stanley (1970). It is unclear what the anterior up shell orientation means and additional observations of living specimens is needed.

### *Conchocele bisecta* (Conrad)

*Life habit.* This species is a large-sized thyasirid in the North Pacific. The life position has not been described. Kauffman (1967) illustrated the life position of a member of the same family, *Thyasira flextuosa* (Montagu) as a vertical, beak up orientation, based on the ecological description by Allen (1958).

*Mode of fossil occurrence.* Eleven individuals were observed in the silty sand of the middle Pleistocene Kakinokidai Fomration at Kawayatsu (Table 2). Most of the individuals are oriented vertically, with the antero-dorsal part upward. This orientation is roughly similar to, but clearly different from the beak up orientation illustrated by Kauffman (1967) for *T. flextuosa.* The preserved orientation of the antero-dorsal part upward seems to be the easiest way to position inhalant mucus tubes upward. Direct observation of living specimens in the substratum is necessary to determine the normal life position of *Thyasira* species.

### *Lucinoma annulata* (Reeve)

*Life habit.* This is a small lucinid species living in the western Pacific. It is *a common* bivalve distributed in muddy substrata in protected environments, but its life position and other ecological properties have not been described. Stanley (1970) described life positions of some lucinids, including *Codakia orbicularis* (Linnaeus), *Phacoides pectinatus* (Gmelin), *Phacoides muricatus* (Spengler) *Anodontia alba* Link and *Lucina pensylvanica* (Linnaeus). They were observed to be buried in the substrata with their beak-upward. Only *L. pensylvanica* was oriented with its antero-dorsal portion wpward.

*Mode of fossil occurrence.* Five individuals were observed in the very fine sand of the Late Pleistocene Kiyokawa Formation at Nagayoshi (Table 2). Four out of the five individuals were oriented vertically, with their antero-dorsal por-

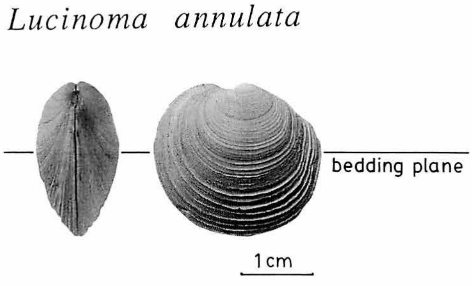

**Fig. 2.** Preserved life orientation of *Lucinoma annulata.* Note that the antero-poterior axis is inclined, so that the anterior part is oriented upward.

tion upward (Fig. 2). This orientation is similar to that of *L. pensylvanica,* as described by Stanley (1970).

**_Lucinoma aokii_ Hirayama**

*Life habit.* This is an extinct lucinid, with a large shell. Information on life positions of similar lucinid species are available from Stanley (1970) as stated in the preceding section.

*Mode of fossil occurrence.* Orientations of 14 individuals of this species were measured in the silty sand of the middle Pleistocene Kakinokidai Formation, at an outcrop in the tunnel of Kawayatsu, Kimitsu-gun (Table 2). Thirteen out of the 14 individuals were conjoined, and nine out of the 13 conjoined individuals were oriented vertically to the bedding. This indicates that post-mortem reworking or bioturbation was minimal during deposition of this shell bed, and nearly all the vertical, conjoined individuals can be regarded as being in their life position. Six out of the nine vertical, conjoined individuals are oriented with the antero-dorsal part upward (Fig. 2). This orientation is interpreted as the preserved normal feeding orientation of this species.

**_Anodontia stearnsiana_ Oyama**

*Life habit.* This is a thin-shelled, well-inflated lucinid, in muddy substrata in protected bay. Life orientation of this species has not been observed. Stanley (1970) described the life position of a member of the same genus, *Anodontia alba.* It was observed to be oriented vertically, with the beak upward, at depths of more than 20cm.

*Mode of fossil occurrence.* Only two individuals were found in the Holocene deposits distributed in the Taitozaki (Table 2), near the southern end of Kujukuri beach. Preserved life position is vertical, with the beak position upward (Fig. 3).

*Anodontia stearnsiana*

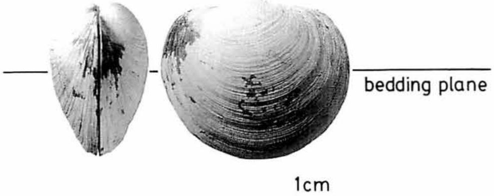

**Fig. 3.** Preserved life orientation of *Anodontia stearnsiana.* The antero-posterior axis is nearly horizontal.

**_Clinocardium braunsi_ (Tokunaga)**

*Mode of fossil occurrence.* This is one of the rare examples of an extinct Quaternary bivalve occurring in the middle to late Pleistocene shallow marine deposits in southern Kanto. It has a large shell with strongly projecting radial ribs. This species is not rare, but conjoined specimens are seldom found. Only a single specimen of 10.5 cm shell length was found in the pebbly sand of the basal part of the Kiyokawa Foramtion at Nagayoshi (Table 2), and it was oriented vertically, with the posterior portion upward (Fig. 4). The orientation is consistent with the life orientation of many living cardiids (*e.g.,* Stanley, 1970).

*Clinocardium braunsi*

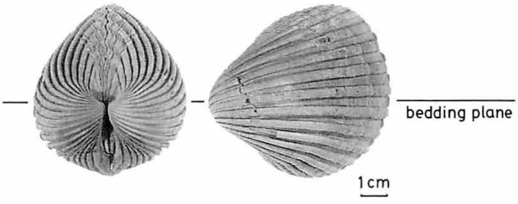

**Fig. 4.** Preserved life orientation of *Clinocardium braunsi.*

**_Saxidomus purpuratus_ (Sowerby)**

*Life habit.* This is a large-sized venerid found in shallow subtidal, mostly gravelly, substrata. There is no description of life position of this species, although it is a very common species around Japan. As the pallial sinus is deep, this species is probably a deep burrower.

*Mode of fossil occurrence*: Observations were made in the sandy silt of the middle Pleistocene Jizodo Formation at Izumiyatu, in the pebbly sand of the late Pleistocene Kiyokawa Formation at Nagayosi, and in the basal part of the Holocene deposits at Taitozaki (Table 2). At the former two localities, this species occurs in a vertical, posterior-up position in soft sediments (Figs. 5, 6). At Taitozaki, this species occurs within burrows in semi-consolidated basement mudstone of deep sea origin in the Kiwada Formation . A

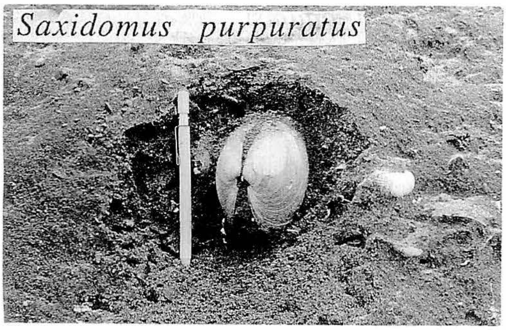

**Fig. 5.** A field photograph of *Saxidomus purpuratus* preserved in life position in the gravelly sand of the middle Pleistocene Kiyokawa Formation at Nagayoshi, Sodegaura-machi. The bedding plane is horizontal.

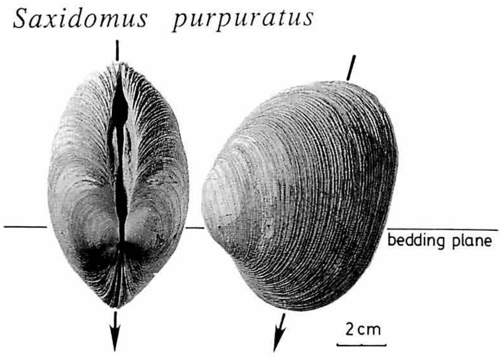

**Fig. 6.** Preserved life orientation of *Saxidomus purpuratus*.

similar occurrence, showing a boring habit of this species, was reported by Matsushima and Ohshima (1974) and Matsushima and Yoshimura (1979).

***Dosinorbis japonicus* (Reeve)**

*Life habit.* This is a common venerid, living in lower intertidal and shallow subtidal sandy substrata in Japan. Kondo (1987b) described the life position of this species, as a vertical, posterior-up orientation. Depth of burial ranges from 2 to 15cm.

*Mode of fossil occurrence.* Observation was made in the basal part of the Kiyokawa Formation at Nagayoshi (Table 2). Conjoined specimens of this species occur parallel to the bedding plane in most cases. Only three out of more than 30 conjoined specimens are found vertical to the bedding. Two specimens show probable life orientations; one of the two specimens a juvenile specimen of 3.3cm shell length is oriented roughly vertical, with the posterior upward. The remaining specimen is oriented vertical, with the anterior-upward. It is unclear whether this orientation is an orientation during escape from a burial event or a fortuitous life orientation.

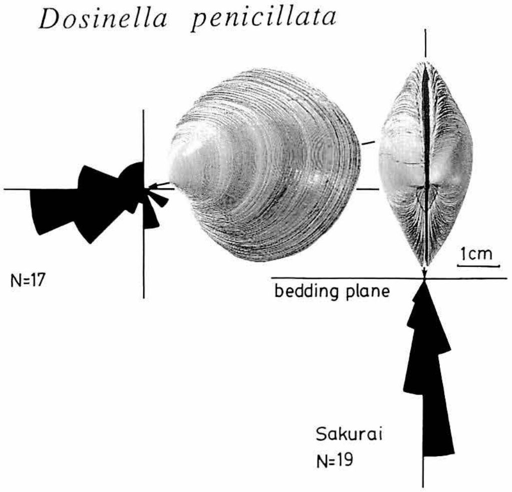

**Fig. 7.** Preserved life orientation of *Dosinella penicillata.*

***Dosinella penicillata* (Reeve)**

*Life habit.* This is a common venerid living in the muddy substrata in protected bay around Japan. The life position of this species has not been decribed.

*Mode of fossil occurrence.* This species is commonly found in life position in the inner bay muddy deposit, which is common in the Holocene drowned valley in Chiba Prefecture. Observations were made in two localities: the Holocene mud exposed along the river side of Iwasegawa, at Kinu and the late Pleistocene Kioroshi Formation at Sakurai (Table 2). At Kinu, 26 conjoined specimens were observed, out of which 19 were vertical, and the rest were oblique or horizontal. Beak positions were variable among vertically oriented specimens; nine specimens were in posterior-up orientation, 10 were in beak-down orientation. At Sakurai, however, beak positions were slightly different: most of the specimens were oriented with their posterior and beak upward, and beak-down positions were much rare (Fig. 7).

***Callista chinensis* (Holten)**

*Life habit.* This is a common venerid, living

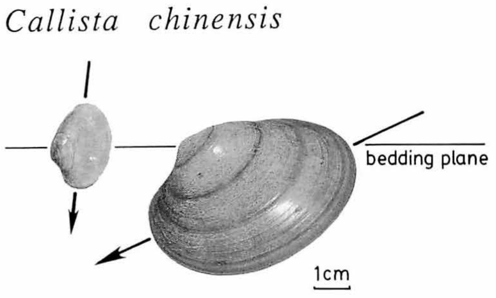

**Fig. 8.** Preserved life orientation of *Callista chinensis*. Note the difference in the inclination of the long axis between adult and juvenile specimens.

in the upper sublittoral zone in the western Pacific. Life position of this species was observed in the laboratory using living specimens collected from Maizuru Bay, north of Kyoto: It is oriented vertically, with the beak to posterior portion upward. The Long axis of the shell was tilted 40° -50° from the horizontal.

*Mode of fossil occurrence.* Observation was made in the basal part of the Kiyokawa Formation at Nagayoshi (Table 2). This species occurs mostly parallel to the bedding plane. Only three specimens were found vertical to the bedding; a juvenile specimen of 1.5cm shell length was oriented roughly vertically, with the posterior portion upward. The long axis was nearly vertical. Another specimen of 6.2cm shell length was oriented roughly vertically, with the beak-posterior portion upward. The long axis was tilted anteriorly 20° from the horizontal (Fig. 8). The remaining specimen was oriented vertical, with the anterior -upward.

***Paphia undulata* (Born)**

*Life habit.* This species commonly occurs in shallow subtidal muddy substrata in Japan. The life position of this species was observed in the laboratory, using specimens from Tokyo Bay: It assumes vertical, posterior-up orientation, with the long axis slightly tilted.

*Mode of fossil occurrence.* Only a single specimen was found in life position in the Holocene mud bed along the River Iwasegawa, Futtsu-shi, Chiba (Table 2). The preserved life position is a vertical, posterior-up orientation, with the long axis tilted 35°-40° from the vertical.

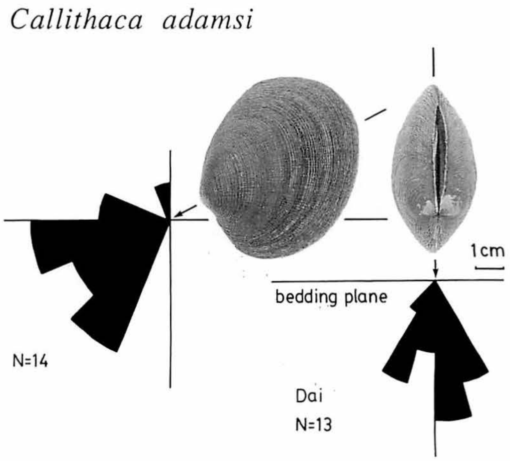

**Fig. 9.** Preserved life position of *Callithaca adamsi.*

***Clementia papyracea* (Gray)**

*Life habit.* This is a thin-shelled, well inflated venerid. The life position of this species has not been described. A deep burrowing habit is inferred from the deep pallial sinus.

*Mode of fossil occurrence.* A single individual was found in life position in the Late Pleistocene Kiyokawa Formation at Nagayoshi (Table 2). The preserved life orientation is vertical, posterior-up, the same as the orientation commonly assumed by most infaunal suspension-feeding bivalves.

***Callithaca adamsi* (Reeve)**

*Life habit.* This is a medium-sized venerid, common in northern Japan. The life orientation of this species has not been described. It is, however, safely inferred that this species assumes a conventional, vertical, posterior-up life orientation.

*Mode of fossil occurrence.* Fourteen conjoined specimens were observed in the Izumiyatu fossil bed of the Jizodo Formation (Table 2). All of the specimens were found in a hydrodynamically unstable, vertical or oblique position. Most of them show posterior-up orientations (Fig. 9). Inclination of the commissure plane varies more than other examples described in this paper. Beak positions are also variable. A single specimen was found vertical, with the anterior upward.

***Raeta pellicula* (Reeve)**

*Life habit.* This is a thin-shelled, well-inflated mactrid. The life orientation of this species

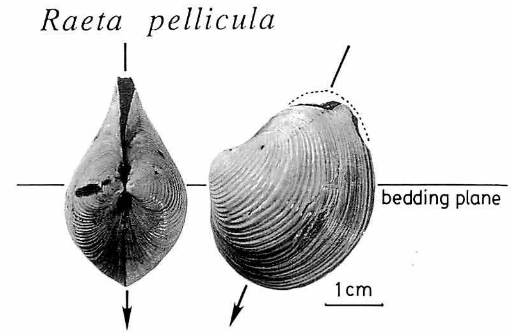

**Fig. 10.** Preserved life orientation of *Raeta pellicula.*

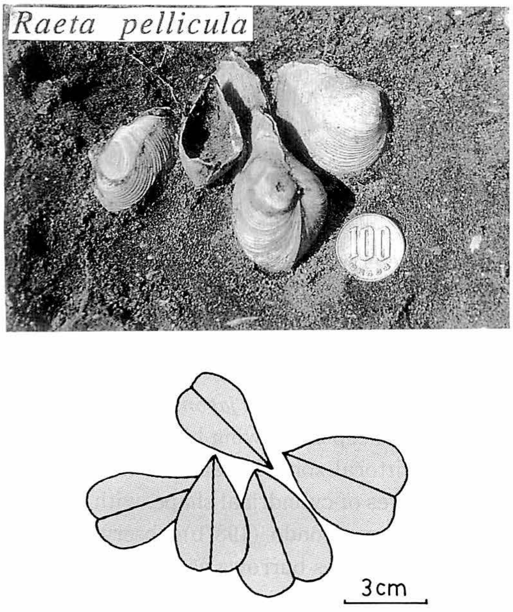

**Fig. 11.** A field photograph showing colonial occurence of *Raeta pellicula* (upper), and a sketch in plan view (lower).

has not been described.

*Mode of fossil occurrence.* Nine specimens were found in their life position at Yoshitaka, Tsurumaki and Nagayoshi (Table 2). Preserved life position of this species is vertical, with their posterior upward. Its long axis is tilted (Fig. 10). An unusual patchy distribution was found in the Kioroshi Formation at Tsurumaki, where five individuals were found in a small colony (Fig. 11). Each individual is oriented so that their ventral margins are close to each other.

***Tresus keenae* (Kuroda et Habe)**

*Life habit.* This is a deep-burrowing bivalve, with very large shells. The life position of this species has not been observed, probably due to the difficulty of observaiton of deep burrowing bivalves. Pohlo (1964) described a vertical, long-axis-inclined living position for *Tresus nuttalli* (Conrad), a similar northeastern Pacific species, on the mud flats in Tomales Bay, California. An adult specimen shows an inclined life position, while it is nearly vertical in juveniles. Stanley (1970) also found a similar phenomenon, describing the life position of the living individuals belonging to the same family, *Mactra fragilis.*

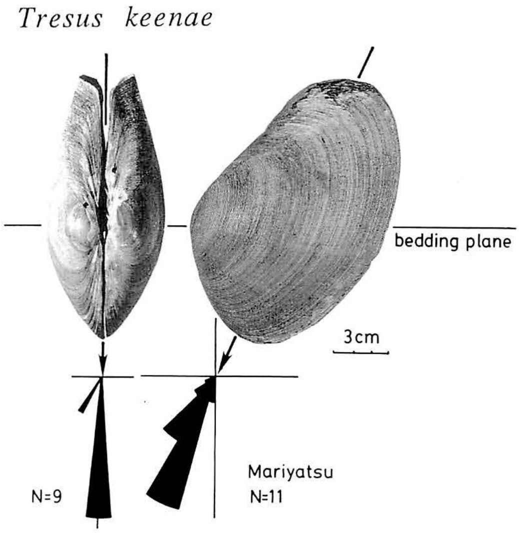

**Fig. 12.** Preserved life orientation of *Tresus keenae.*

*Mode of fossil occurrence.* Fifteen individuals were observed in the very fine sand of the middle Pleistocene Yabu Formation at Mariyatsu (Table 2), out of which 11 were found in a vertical life position. The life position of this species is similar to that of *Panopea japonica* and *Mya arenaria,* but it differs in its distinctly inclined long axis from the vertical. The long axis of this species inclined 30° on the average, although it varies from 0° to 70° (Fig. 12).

***Solen krusensterni* Schrenck**

*Life habit.* This is a common solenid species, found in shallow subtidal settings in Japan. There is no description of the mode of life of this species. It is, however, possible to infer the life habit of this species by analogy with a similar species *Solen strictus,* a common intertidal species described by Frey *et al.* (1988) from Korea. *Solen strictus* lives in a deep vertical burrow lined with

**Fig. 13.** A field photograph of *Panopea japonica* preserved in life position in the very fine sand of the middle Pleistocene Yabu Formation.

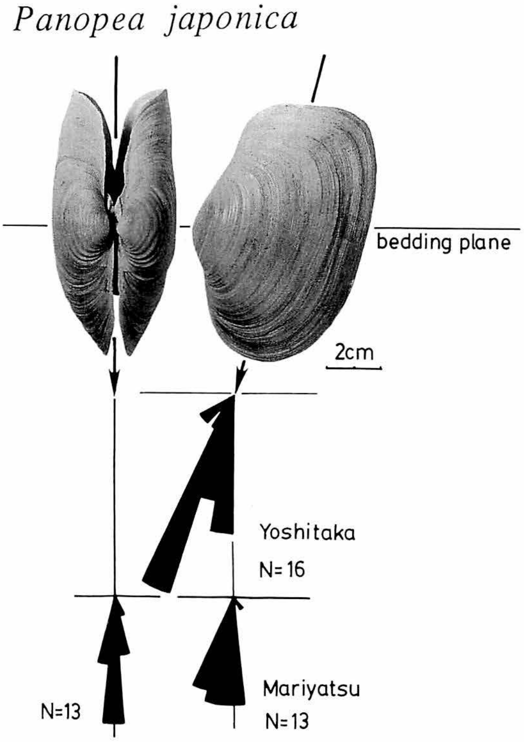

**Fig. 14.** Preserved life position of *Panopea japonica.*

mud, up to 50 cm long. In general, the burrows are tilted about 15° from the vertical.

*Mode of fossil occurrence.* Several individuals were found in their life position at Mariyatsu and Nagayosi (Table 2). The preserved life position of this species is vertical, posterior-up, with its long axis about 20° from the vertical. Burrows were not recognized around the *in situ* specimens.

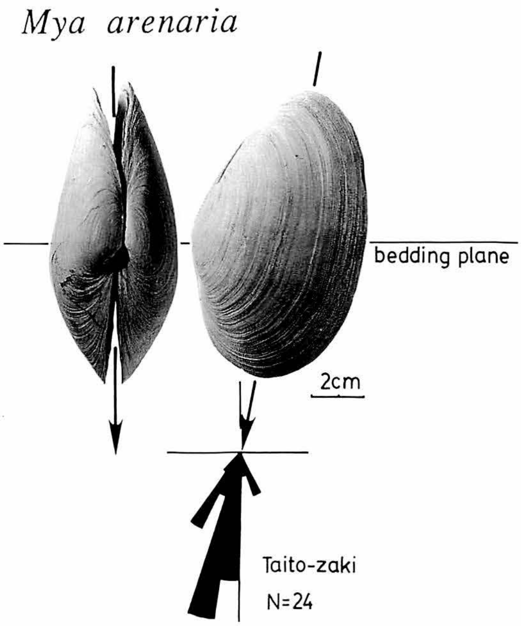

**Fig. 15.** Preserved life position of *Mya arenaria oonogai.*

***Panopea japonica* A. Adams**

*Life habit. Panopea japonica* is an almost immmobile, deep-burrowing bivalve, living in the upper sublittoral zone. It has well-inflated, thin-shelled valves of cylindrical shape, with pedal and siphonal gapes. Kondo (1987b) observed a specimen of this species burrows as deep as four times shell length in the laboratory. Inclination of the long axis has not been observed.

*Mode of fossil occurrence.* This is one of the commonest bivalve species found in its life position in the Quaternary deposits of Chiba Prefecture. Observations were made at the middle to late Pleistocene deposits at Nagayosi, Otake, and Mariyatsu. Five out of six individuals of this species are found in vertical life positions in pebbly sand at Nagayosi. Similarly, 14 out of 16 at Mariyatsu, and 13 out of 16 at Otake are found in their life position.

Preserved life orientations of this species are vertical, posteriorup orientation, with the truncated posterior portion parallel to the bedding. Inclination of the long axis of the shell varies from −5° to 25° anteriorly from the vertical (Fig. 13 and 14). The slightly tilted shell orientation is interpreted as a result of vertical disposition of the long siphon.

***Mya arenaria oonogai*** **Makiyama**

*Life habit.* This is a deep-burrowing bivalve, living in intertidal sand-mud flats. The life position of living individuals of this species has been observed by some authors (Medcof, 1950; Goshima, 1982). According to them, this species is buried in the substratum with its long axis nearly vertical or slightly tilted ventrally.

*Mode of fossil occurrence.* Twenty fjve individuals of this species were observed at Taitozaki (Table 2), 24 of which were found preserved in a vertical, posteriorup life position. Inclination of the long axis ranges from -20° to 40°, but most of the measurements fall within the range of 0° to 25° (Fig. 15).

The orientation of the long axis of the fossil examples appears to be more inclined as compared to those observed for living individuals.

***Periploma otohimeae*** **Habe**

*Life habit.* This is a deep water periplomatid species living around Japan. Ecological observation of this species or other species of the genus have not been made.

*Mode of fossil occurrence.* Twenty five individuals of this species were observed in the middle Pleistocene Kasamori Formation, at Tabi (Table 2). They were all oriented parallel to the bedding, with their right valve upward. This is safely interpreted as their life position, in spite of being similar to the hydrodynamically stable orientation on being exposed on the sea bottom.

The horizontal life position of this species may indicate deposit-feeding life habit, being similar to most tellinids. A horizontal life position within the substratum has been interpreted as an adaptation to active movement, which is necessary for deposit-feeding (Holme, 1961; Stanley, 1970).

## Discussion: Taphonomic and Paleoecologic Implications of Preserved Life Positions of Soft-Bottom Infaunal Bivalves

The information on the preseved life positions can provide insight into many studies including taphnomy and paleoecology of the bivalves. To clarify the meanings of preserved life position, it is appropriate to examine factors determining the presrevation.

The most important factor determining the preservation of life position is depth of shell burial within the substratum, as suggested by Fürsich (1980) and Kondo (1987a). Most of the bivalve species described above are deep burrowers. The described life positions of shallow burrowers, such as those of *Clinocardium braunsi*, may be taken for fortuitous examples. Shallow burrowers are usually preserved in reworked, hydrodynamically stable positions in shallow-sea sediments like those of the Shimosa Group.

Kondo (1987a) attributed selective preservation of life position of deep-burrowing bivalves, to sea floor erosion probably of storm origin. The depth of erosion in shallow-sea sandy botttom was estimated to be 15-20cm from the sediment surface. Only extremely deep burrowers, such as *Panopea japonica* and *Tresus keenae,* which are buried more deeply, are usually preserved in life positions. Most bivalves buried at shallower positions are reworked on the sea floor and oriented in hydrodynamically stable positions.

Another factor controlling preservation of life position relates to environmental conditions, such as depth of storm erosion. In general, the depth of storm erosion is greater, as the environment becomes shallower and being more exposed to open sea.

Two bivalves *Dosinorbis japonicus* and *Dosinella penicillata* are preserved in a contrasting manner, in spite of the similar shell morphology and similar depth of burial. It is common for *D. penicillata* to be preserved in life position, while *D. japonicus is* rarely preserved in life position. *Dosinella penicillata* lives in the shallow-sea mud bottoms of embayment. In contrast, *D. japonicus* lives in sandy bottoms in similar shallow seas. Diferent depth of erosion is probably the main factor producing their contrasting modes of preservation.

Bioturbation effects are interpreted as being negligible in the cases where the shells are large enough: Bivalves with shells larger than 3-5cm are found in their life orientation or physically stable reworked orientation, with only small variations, while small bivalves less than 3cm are susceptible to probable bioturbation effect. Compaction may have modified the original life positions, as Fürsich (1980) pointed out. In some individuals, minor differences were recognized between living and fossil life positions, *e.g.,* in the inclination of the long axis of large-sized, deep

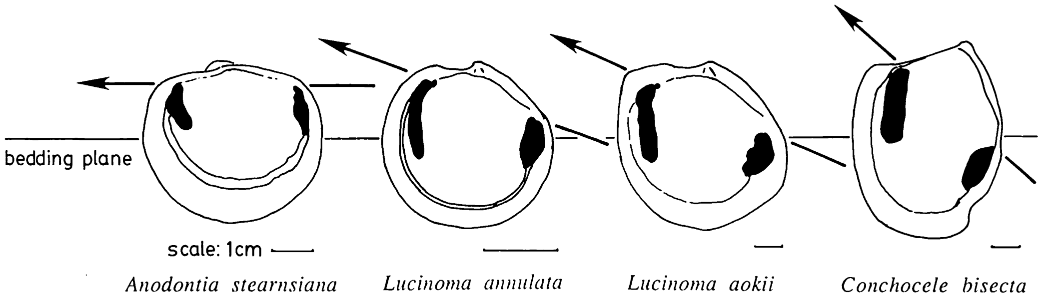

**Fig. 16.** Life orientations of some lucinaceans. Schematic drawings of left lateral view. A: *Anodontia stearnsiana,* B: *Lucinoma annulata,* C: *Lucinoma aokii,* D: *Conchocele bisecta.* Each arrow shows antero-posterior axis.

burrowing bivalves, such as *Panopea japonica, Tresus keenae* and *Mya arenaria.* The inclination of their long axis was observed to be larger than that observed in living specimens. Sometimes their shells were found nearly horizontal, with the commissure plane still being vertical.

As discussed above, preservation of life position is strongly influenced by the environmental conditions as well as the ecological characteristics of the species. If the life orientation and depth of burial are reconstructed properly, systematic analysis on preservational trends in the bivalve life position will provide information on the paleoenvironments and diagenetic conditions, which cannot be obtained from other conventional observations (Kondo, 1987a; 1989). Conversely, if we compare the preservational condition of bivalve life position in the same shell bed, the observed difference can be taken for the difference of autoecology of each bivalve.

Another implication of the preserved life position include causes of death of the animal, as suggsted by Ager (1963, p.83). Observed life positions of soft-bottom infaunal bivalves are mainly consistent with those observed on living individuals or those inferred by analogy with similar species. No serious discrepancies were found between fossil and living life positions. In most examples, the observed orientation agree well with the normal life position, that is, the feeding orientaiton. There are, however, a few examples showing a hydrodynamically unstable orientation, but different from normal life orientation for such species as *Dosinorbis japonicus, Callista chinensis, Callithaca adamsi.* The anterior-up orientation is similar to the inverted erect probing orientation assumed during escape upon anastrophic burial. It is, however, uncertain whether the orientations were assumed due to such a burial event. Such escape orientations can be properly recognized only when most of the fossil individuals concerned are in the anterior-up orientations within a bed with characteristic sedimentary features of rapid burial.

Preservation in normal life position indicates that the animal died in normal feeding orientation; it died neither of attack by predators nor of such physical disturbances as those found during periods of severe storms. After death, the position and orientation have not been shifted or rotated by biological or physical agents, and have not been exposed to erosion.

Preserved life orientation of bivalves is well worth being documented, also because it is one of the important expressions of the ecology of the animal, particularly for extinct species. As an example, life positions of lucinaceans are briefly discussed below from the viewpoint of relations among shell form, life position and the ecology.

Stanley (1970) found some relationships between shell form and life position in bivalves of various life habits including soft-bottom infaunal dwellers. Some examples described above can add new information on this field of study.

Life orientations of lucinacean bivalves appear to be grouped into two types: One is a beak-up orientation shown by *Anodontia stearnsiana* and the other is an orientation with the antero-dorsal part upward shown by *Lucinoma annulata, L. aokii,* and *Conchocele bisecta* (Fig. 16). It is notable that the latter three lucinaceans have a pointed anterior and tend to orient the anterior upward. In contrast, *A. stearnsiana* has a relatively rounded anterior and the antero-posterior axis is nearly horizontal.

Stanley (1970) described the life positions of seven lucinacean species: *Diplodonta notata, Codakia orbicularis, Phacoides pectinatus, P. muricatus, Anodontia alba* and *Lucina pensylvanica*. Excluding *D. notata* which shows an unusual upside-down life orientation, only *L. pensylvanica* assumes an orientation with its antero-dorsal part upward. In life position, the anterior mucus tube passes almost vertically upward, and the posterior siphon passes downward to discharge into the coarse sediment(fig. 34, Stanley, 1970). The remaining species, on the other hand, show a beak-up orientation, and discharge on the sediment surface. Stanley (1970) suggested that a pointed anterior of lucinacean shells indicates an anterior-up life position. The four examples described in this paper support Stanley's suggestion.

## Acknowledgments

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## 地層中に保存された砂泥底生内生二枚貝化石の生息姿勢 —— 千葉県の第四系からの記載

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千葉県の第四系に産する砂泥底生内生二枚貝化石のうち，生息時の姿勢を保持していると考えられる19種について，それらの地層面に対する方向を計測した．また，一部の種については，これらの方向性と現生個体での観察結果との比較を行った．これらの多くは現生種であるが，ツキガイ超科やリュウグウハゴロモガイ科の二枚貝など，生息姿勢も含めてその生態があまり知られていない種が多い．地層中で観察された二枚貝化石の方向性は，同種の現生個体で観察された摂餌時の姿勢とほとんどの場合一致し，生息時の姿勢をよく保持していることが分かった．ただし，生息姿勢と異なり，しかも物理的に不安定な姿勢も少数観察された．

生息姿勢が保存されている二枚貝のほとんどは，深潜没生活者であるかまたは水流による攪乱の少ない内湾泥底の生息者である．このことは，例えば暴風時の海底侵食のような底質表面の物理的な攪乱が，浅潜没生活者や外洋種が生息位置で保存されることを妨げている主要な要因であることを示す．このほか，生物攪乱や埋没後の圧密も二枚貝化石の生息姿勢を死後変化させることがある．