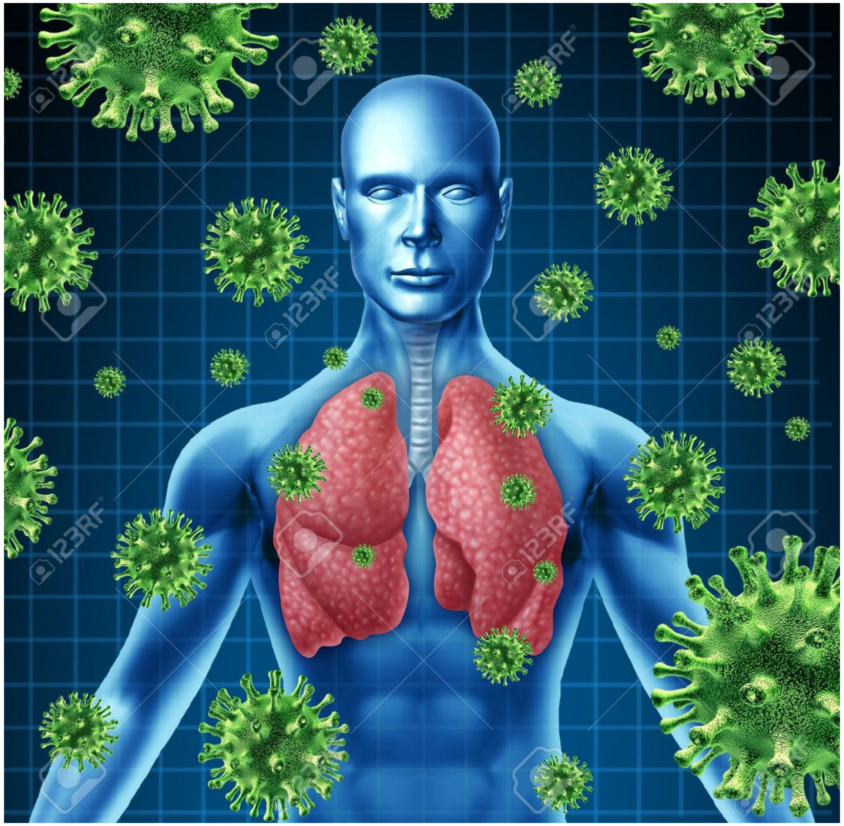
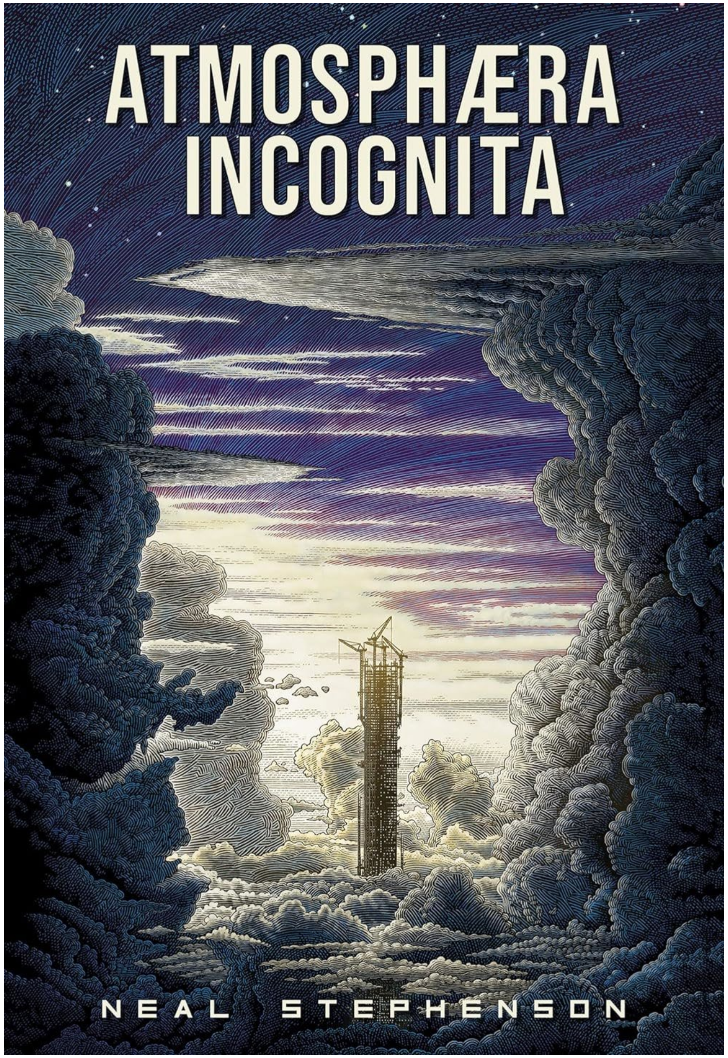
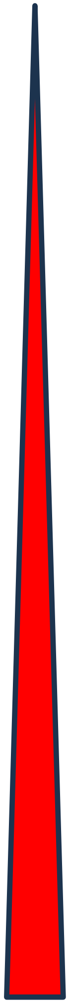
The Air We Breathe







Point 1: Science fiction inspires complex research goals

"Atmosphaera Incognita" by Neal Stephenson

Class Question:
What do you want to know about this tower's ascending altitudes from 0 to 20 km?

Class Questions About 20-km Tower

Particulates gradients? Jeffrey

When does oxygen stop? Elizabeth

Vertigo experienced? Richard

What do I (feel) upon ascending? Diane

Can I see incoming weather systems? Laurie

What is likely to hit tower? Jim

What happens to bird flight, migration? Helen

What is the temperature gradient? Janet

What is combustion particulate gradient? Mark

Solar radiation? Anita

Visual gradient changes from ground up? Joey

Insect life gradient? Kathy

Scientific Inquiry vs Experiential Learning

Human Respiratory System

Lungs = organ exposed to external environment

Breathe 2000 to 3000 gallons of air per day

Air has 1,000 to 10,000 microbes per m^-3

Air has 10-50 ug fine, ultrafine dust per m^-3

Lecture 2 Atmospheric Layers

Troposphere: layering heights upwards depends on latitude

Layer 1-Planetary boundary layer (PBL) rises & falls every 24h
Rise & fall due to daytime solar heating, cooling earth's surface
PBL itself is turbulent as most biologically active layer
PBL concentrates water heat + atmospheric biota
PBL is also an "elevator" or one particle uplifting mechanism
Another mechanism is cumulus cloud formation

Layer 2-Surface inversion "blanket" of warm air above PBL

Layer 3-Clouds "Cloud Appreciation Society"
Cloud altitudes vary with cloud type, season, latitude
Lower altitudes for cumulus, high for cirrus clouds

Layer 4-Tropopause = troposphere ends & stratosphere starts
Layer 5-Stratosphere is the beginning of outer space

Weather Balloon (a radiosonde)

Stratosphere

Troposphere

Lecture 2: Air We Breathe
Experiential, deductive, empirical, scientific methods

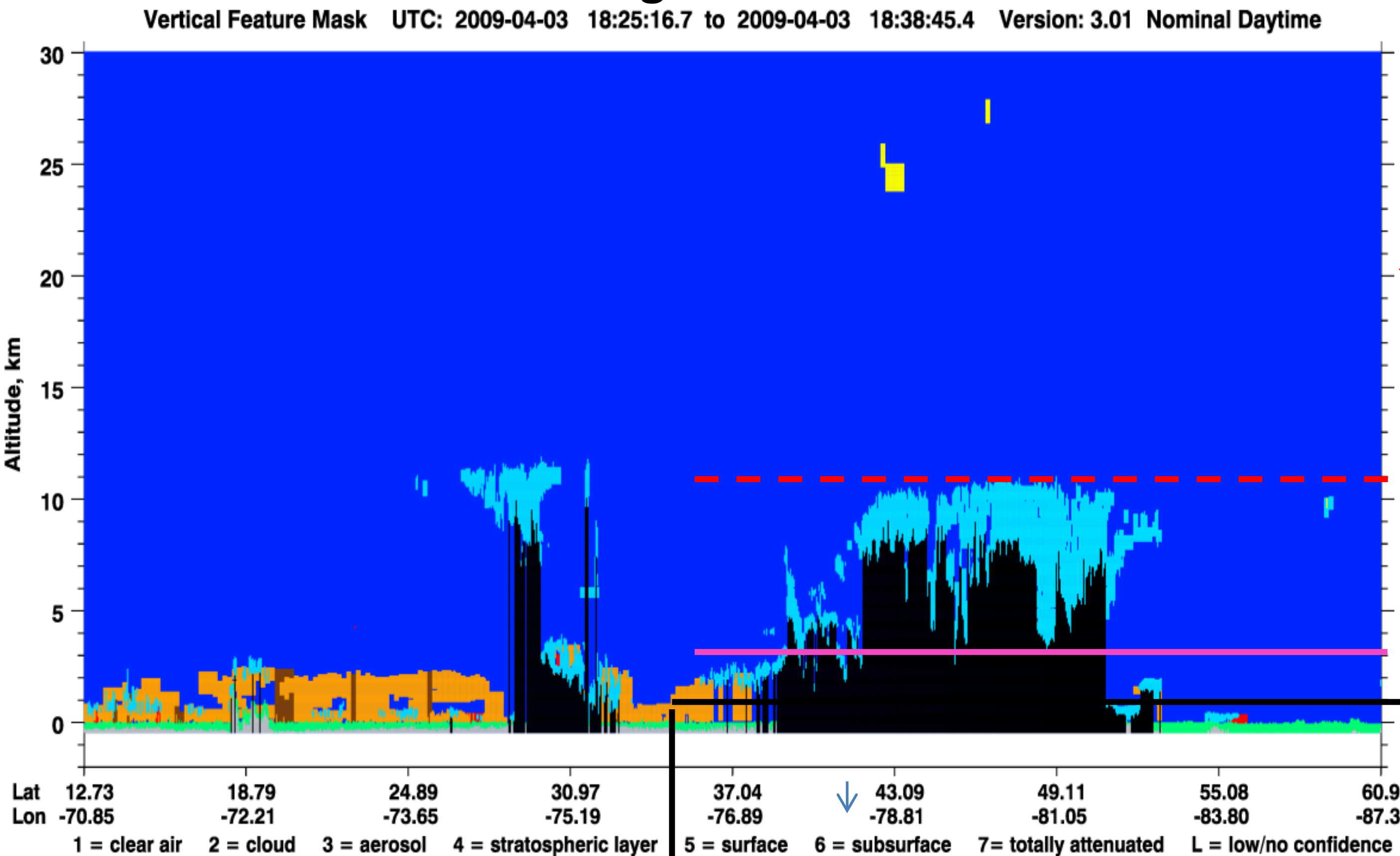
Story 1: Falling out of a plane thru stratosphere. What lifeforms here? Not humans. Two people lived to tell.

Story 2: Lucretius 50 B.C. deduced clouds + storms "The Nature of Things"

Story 3: Citizen science in the "Cloud Appreciation Society" book. Rise of a rainstorm: how cumulus clouds grow into cumulonimbus clouds, lifting particles upward, downward

Story 4: Atmospheric sciences textbook
Water vapor and particle sizes

Ocracoke Island NC lidar image from CALIPSO satellite 700 km above earth



Tropopause 11.3 km

Inversion 2.9 km

Planetary Boundary Layer (PBL) 1.9 km daylight

Clear, sunny day

Surface winds W WSW 29-37 km h^{-1}

Lecture 2 Vertical Atmospheric Gradients

Table II. Daylight atmospheric layers were estimated during peak pine pollen release at Pamlico Sound, NC, USA, using atmospheric profile at 0Z. Data from radiosonde (weather balloon) soundings from Morehead City, NC, 34.70 N–76.70 W (WBAN # 93768 WMO #72305). Data from http://www-frd.fsl.noaa.gov/mab/raob/.

Altitude (m)	Atmospheric pressure (mb)	Temperature (°C)	Dew Pt (°C)	Relative humidity (%)	Actual VPD (kPA)	Wind speed ($m\ s^{-1}$)	Wind speed ($km\ h^{-1}$)	Wind direction	Profile
11	9990	22.2	10.2	46.5	0.16	4.1	14.8	W	Above-ground level
133	9850	21.8	8.8	43.4	0.16	—	—		
588	9340	17.6	6.6	48.4	0.14	—	—		
671	9250	16.8	5.8	48.2	0.13	—	—		
1383	8500	10.0	5.1	71.5	0.13	13.9	50.0	W	
1451	8430	9.4	5.4	76.1	0.13	9.4	33.8		
1759	8120	7.4	2.7	72.0	0.11	—	—		
1932	7950	7.2	−1.8	52.7	0.08	—	—		Daylight planetary boundary layer
1973	7910	8.8	−10.2	24.8	0.04	—	—		
2015	7870	11.0	−38.0	1.7	0	—	—		Inversion
2426	7490	11.0	−38.0	1.7	0	—	—	W	Inversion
2867	7100	7.6	−41.4	1.5	0	—	—		Inversion
2990	7000	7.2	−41.8	1.5	0	19.5	70.2	WSW	Inversion
3072	6930	7.4	−41.6	1.5	0	—	—		Inversion
5650	5000	−13.5	−59.5	0.9	0	29.8	107.3	WSW	Potential mixed-phase cloud layer
6116	4700	−17.3	−61.3	0.9	0	—	—		
7002	4170	−21.7	−64.7	1.4	0	—	—		
7310	4000	−24.5	−66.5	0.9	0	31.9	—	W	
8344	3460	−33.7	−72.7	0.8	0	—	—		
9330	3000	−42.1	−78.1	0.9	0	—	—	W	
10540	2500	−52.3				41.2		W	
11298	2220	−56.7	−77.7	5.1	0	35.5	127.8	WSW	Tropopause

Atmospheric layering du

Weather balloon (radiosonde) reading April 2009 Ocracoke Island NC
Williams C.G. 2019. *Grana*

Lecture 2 Atmospheric Layers + Globally Transported Particles

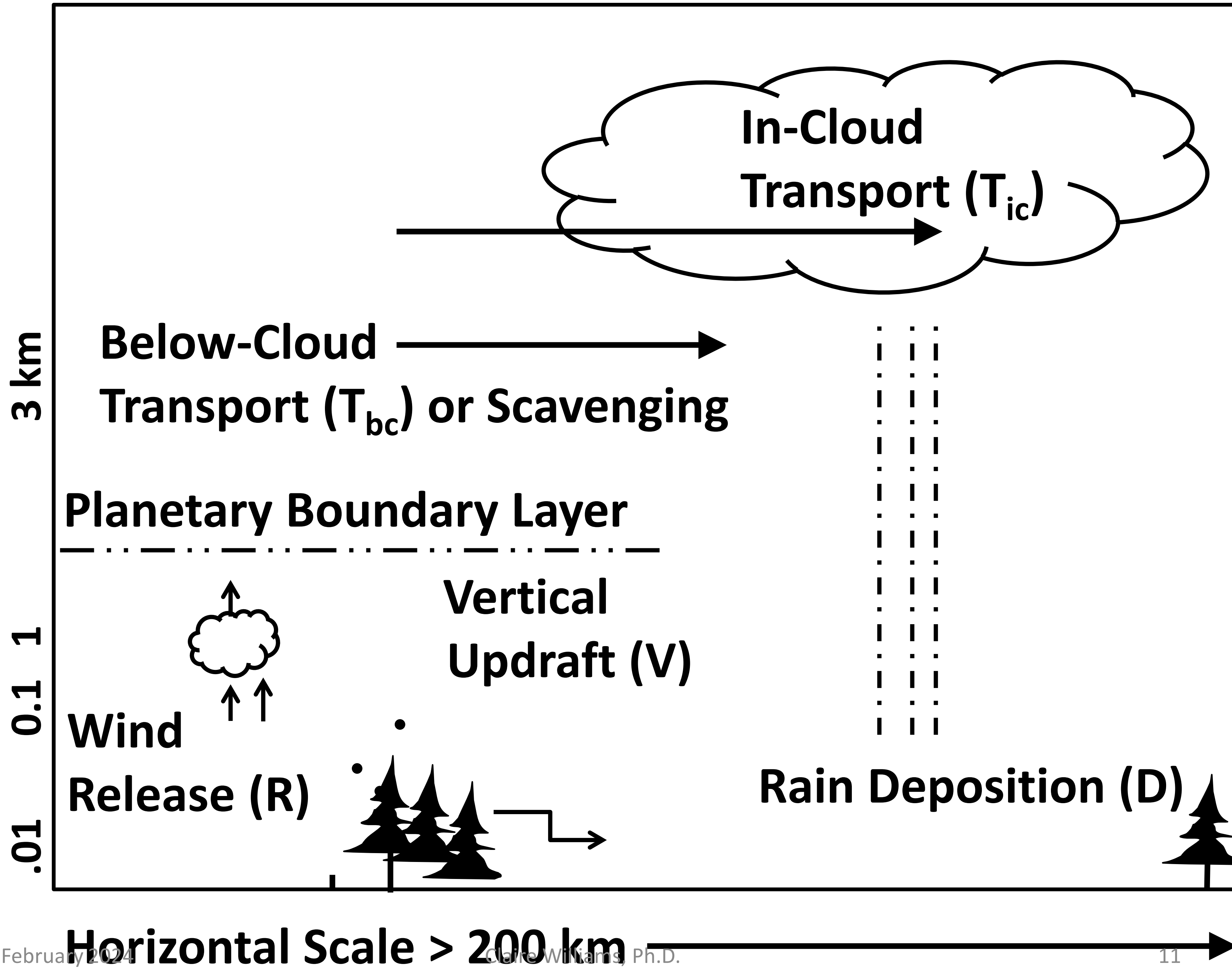
Example: Ocracoke Island NC (Williams 2019)

PBL? 2 km daylight hours, shrinks to 0.7 km night hours in spring
Surface inversion? 2.0 to 3.0 km
Cloud base? 5.6 km
> Below the 20-km tower

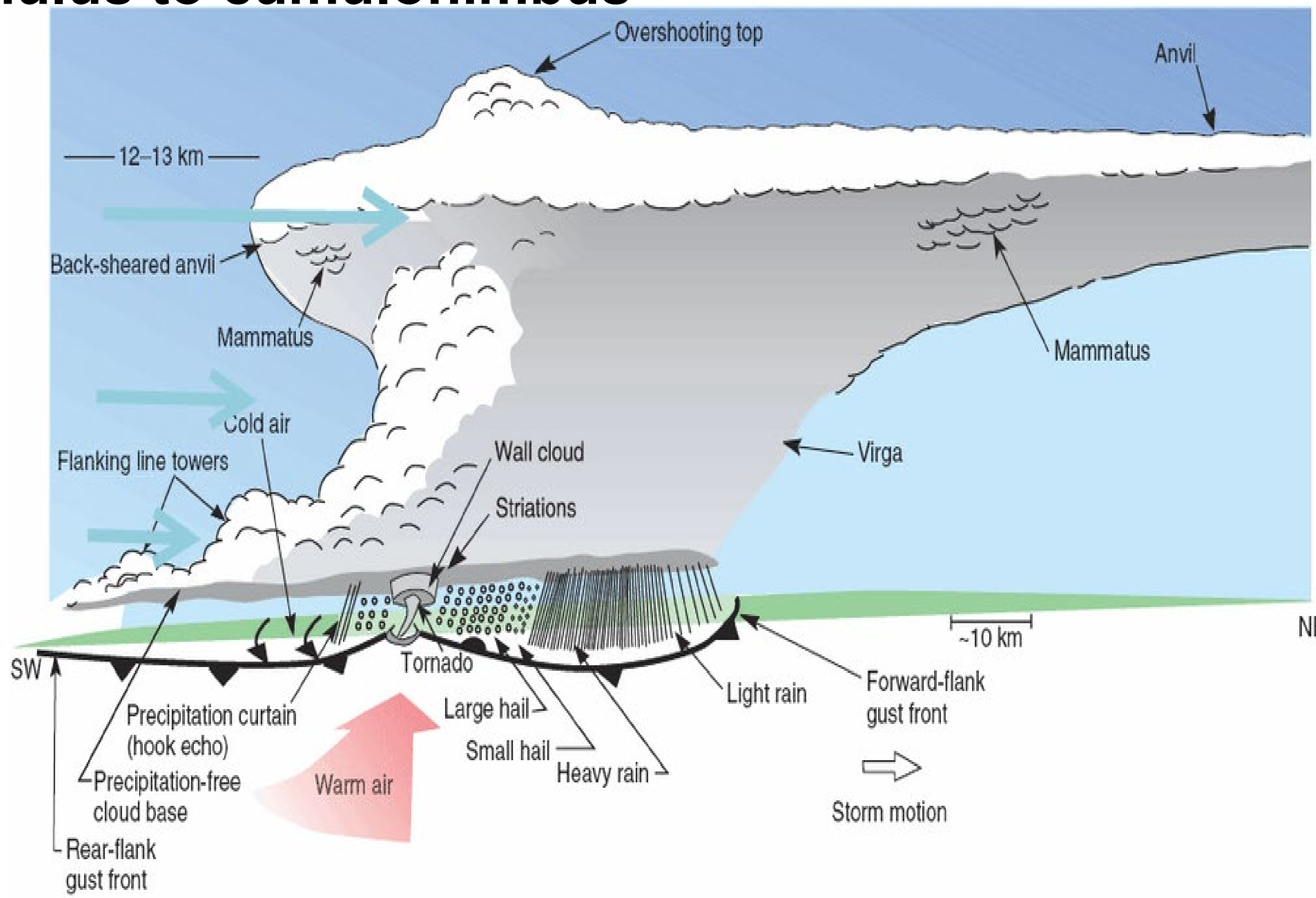
Aircraft altitudes? 10-15 km for jets 17km for high-altitude aircraft
> Below the 20-km tower

Jet stream? 8 km at the poles 18 km at the equator
> Below the 20-km tower

Tropopause? Altitude 11 km at Ocracoke Island NC in spring
> Below the 20-km tower


In-Cloud
Transport (T_{ic})
Below-Cloud
Transport (T_{bc}) or Scavenging
Planetary Boundary Layer
Vertical
Updraft (V)
Wind
Release (R)
Rain Deposition (D)
3 km
0.1 1
.01
Horizontal Scale > 200 km

Lecture 2 Air We Breathe
Global particles: single-cell thunderstorm genesis: cumulus to cumulonimbus



Based on NOAA National Severe Storms Laboratory publications and an unpublished manuscript by H. B. Bluestein. Reprinted from *Cloud Dynamics*, R. A. Houze, p. 279, Copyright (1993), with permission from Elsevier.

Lecture 2 Air We Breathe
How rainstorm formation affects particle load

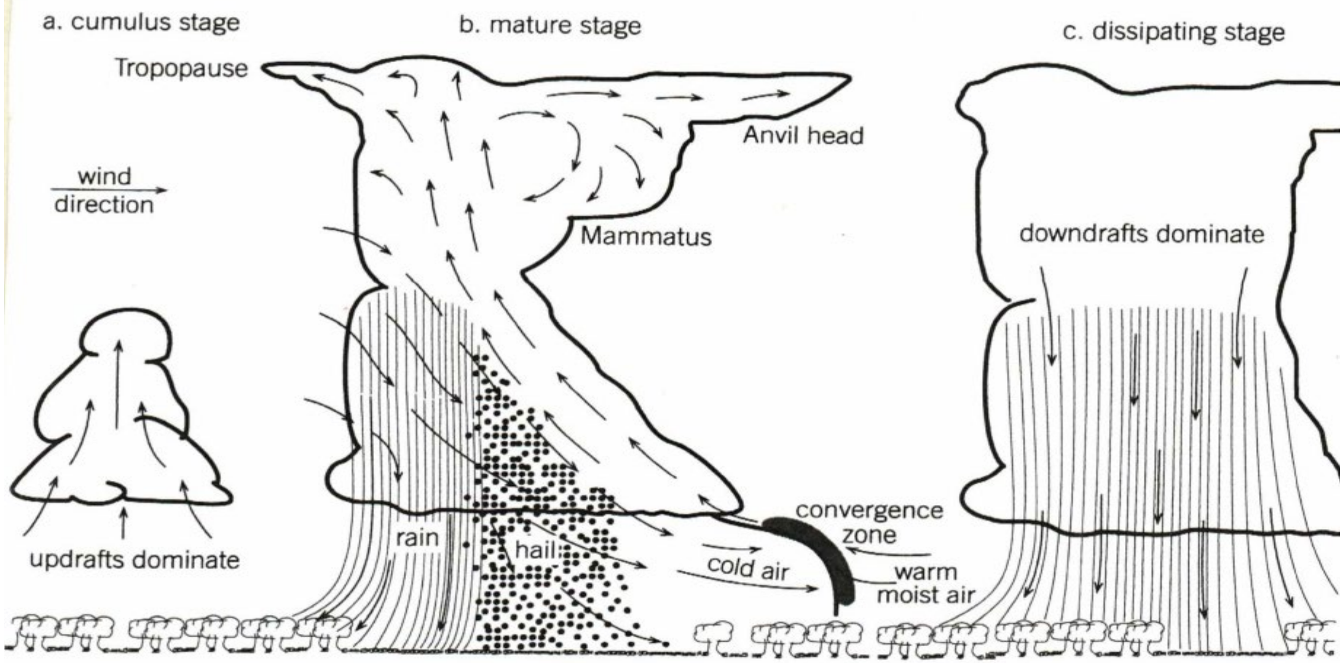
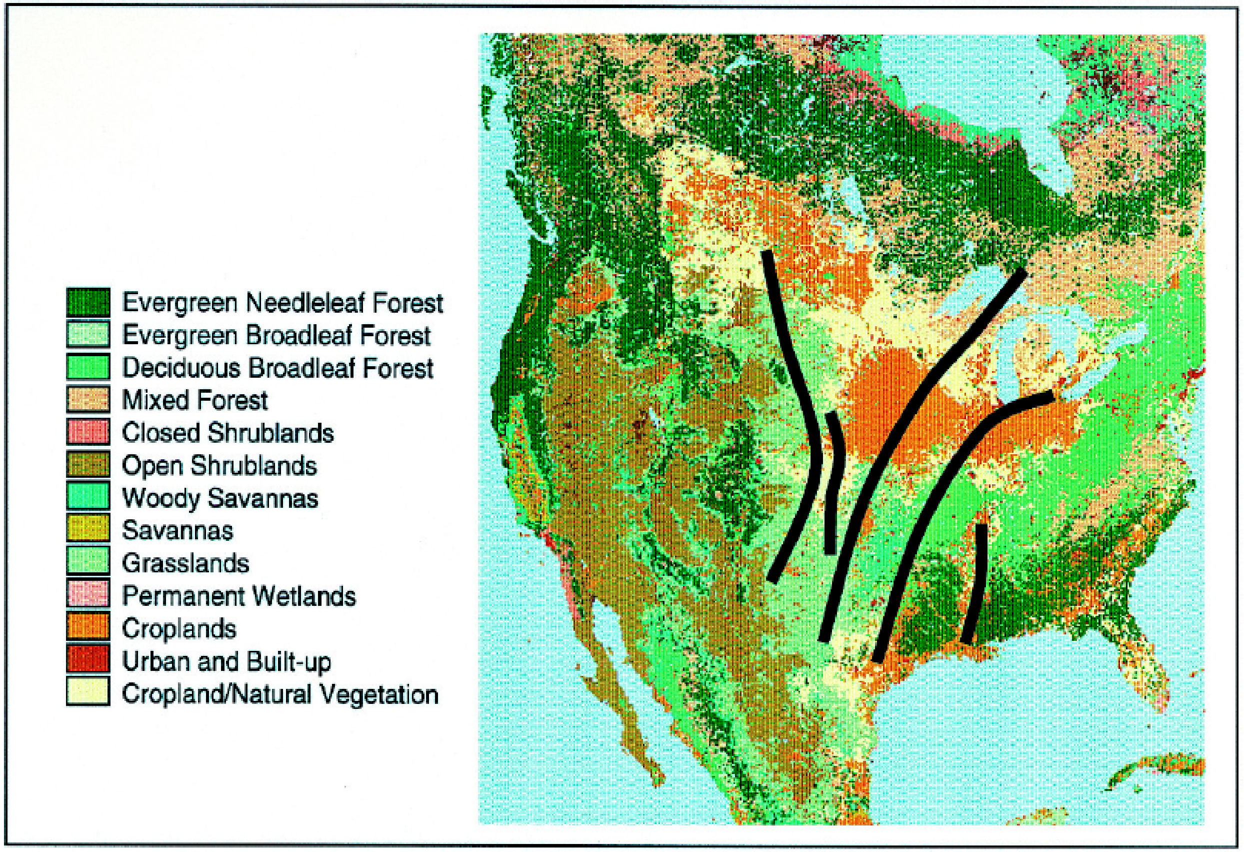


Figure 8.11. Stages of convective storm (thunderstorm) development.

Air-mass thunderstorms tend to develop when the lower atmosphere is highly unstable. Therefore, when v
moist air rises from the surface, condensation quickly occurs, releasing energy and enabling vertical acc
ion of the air within the cumulus cloud (a). The formation of circulation patterns within the convective cell
he mature stage (b). Downdrafts of cold air originating in the upper center of the cell produce a cool c
hat spreads outward above the ground surface and lifts the warm, moist air in front of the cell. A conver
zone develops at the outflow front where biota that resist upward movement can become concentrated.
nent of the cell over warm ground helps to propagate continued activity. The dissipation stage occurs wh
updrafts weaken, reducing the release of latent energy within the cell, and downdrafts prevail.

Isard SA and SH Gage 2001. *Flow of Life in the Atmosphere*. Mich State Press. p. 117.



A wide range of aerobiota (ranging from allergens, fungi, and spores to insects and birds) use the same atmospheric motion systems to move long distances and thus follow similar pathways or atmospheric cor-

Lecture 2: Global Particles & Long-Range Transport

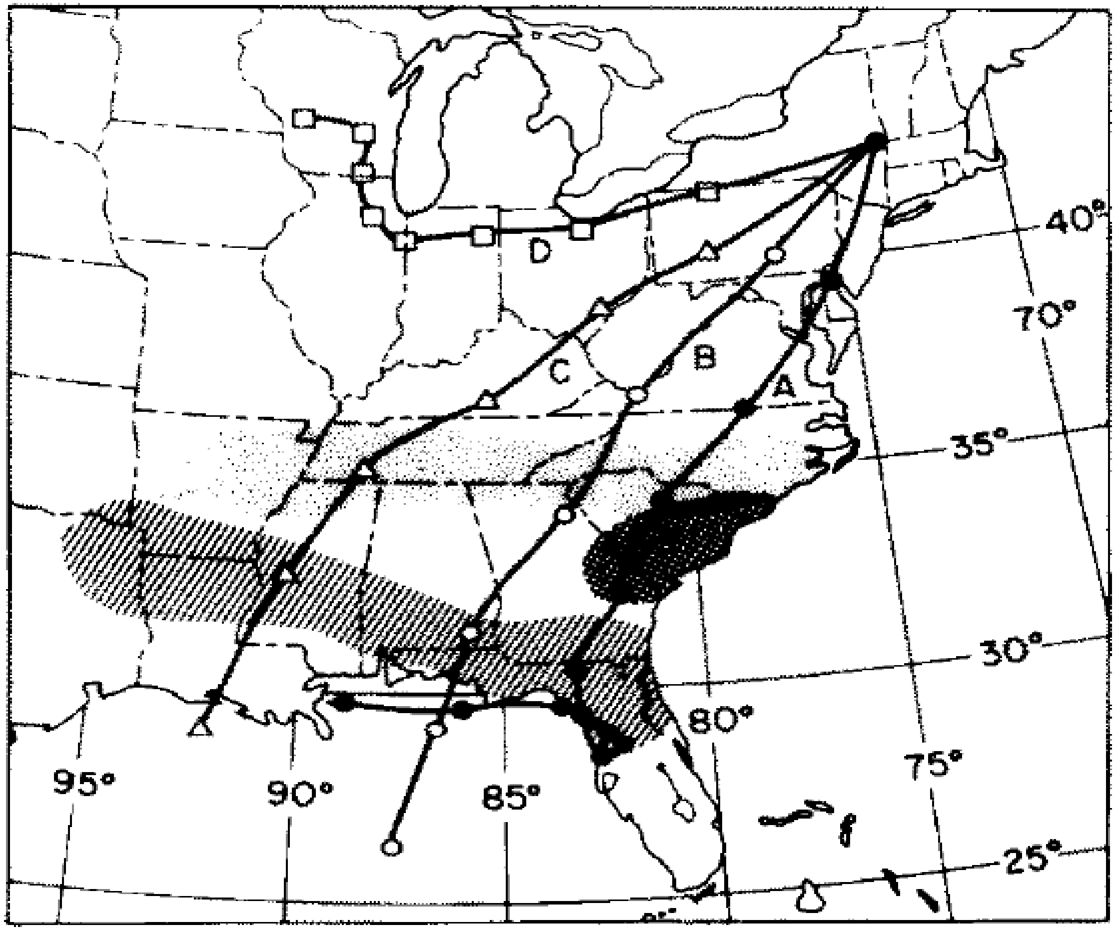


Fig. 10. Probable source regions of *Juniperus* (stippled area), *Taxodium* (hatched area) and mixed pollens (cross hatched area) collected in case 9, 27–28 February 1977 and trajectories ending at Albany during the sampling period: A, 1300; B, 1900; C, 0100 and D, 0700 EST.

Long-range transport
Coarse bioaerosols
Raynor & Hayes (1983)

Cedar fever

Particle Sizes for A Dust Storm’s Contents
Spatial Scales of Inquiry

10^{5} m Dust storm April 13 2011 774,000 km^2
10^{-3} m Raindrop, small (2 mm) to large (6 mm)
10^{-4} m Middle East dust particle (2 to 20 um, 85% PM10)
10^{-5} m Bacteria (0.5 to 4 um)
10^{-5} m Thickness of a human hair (0.08 nm)
10^{-6} m One cloud condensation nucleus (<1 micron)
10^{-10} m One water molecule 3×10^{-10}

Sources: Ledari et al. 2020; Middleton et al. 2017; Rosinski 1966; Griffiths et al. 2012; Després et al. 2012; Jaenicke 2005; Mandrioli et al. 1973; DeMott et al. 2010.

What is in the air we breathe?

Troposphere: *mostly nitrogen with oxygen*
water vapor "we live in the bottom of an ocean of air"
carbon dioxide + other greenhouse gases
ozone
volatile organic compounds
biogeochemical cycle compounds
dust
sea salt
smoke
volcanic ash
micro-organisms, protein molecules, allergens, adjuvants
biological debris: hair, dead skin cells, cellulose, insect parts
industrial & manufacturing waste
transport's combustion engine emissions
tire wear particles

HOW TO SPOT
CUMULUS CLOUDS

Cumulus are low, detached, puffy clouds that develop vertically in rising mounds, domes or towers, and have generally flat bases. Their upper parts often resemble cauliflowers and they appear brilliant white when reflecting high sunlight, but can look dark when the Sun is behind them. Cumulus tend to be randomly scattered across the sky.

TYPICAL ALTITUDES*: 2,000–3,000ft
WHERE THEY FORM: Worldwide, except in Antarctica (the ground is too cold for thermals).
PRECIPITATION (REACHING GROUND): Generally none, except for brief showers from congestus.


Cumulus humilis


Cumulus mediocris


Cumulus congestus

CUMULUS SPECIES:
HUMILIS: Minimal vertical extent. They look flattened and appear wider than they are tall. Do not cause precipitation.
MEDIOCRIS: Moderate vertical extent. Might show protuberances and sproutings at the top. Appear as tall as they are wide. Do not cause precipitation.
CONGESTUS: Maximum vertical extent. The tops are like cauliflowers. Appear taller than they are wide. Cause brief downpours.
FRACTUS: Ragged edges and broken up. Can form in the moist air below rain clouds.

CUMULUS VARIETIES:
RADIATUS: When Cumulus have formed into rows, or 'cloud streets', which are roughly parallel to the wind direction. Due to perspective, the rows appear to converge towards the horizon.


Cumulus mediocris radiatus

NOT TO BE CONFUSED WITH...
STRATOCUMULUS: Cumulus clouds are detached, not joined into a layer like Stratocumulus.
ALTOCUMULUS: Cumulus are not usually as regularly spaced as a layer of the higher Altocumulus. The clouds also look larger than the clumps of the Altocumulus. When they are above the cloudspotter, Cumulus appear larger than the width of three fingers, held at arm's length.
CUMULONIMBUS: which often develops from a large Cumulus congestus. A cloud is still a Cumulus when its upper region has a sharp outline, compared with the softer top of the Cumulonimbus.

* These approximate altitudes (above the surface) are for mid-latitude regions.

Top right: Michael Rubin (member 329). Bottom: Paul Cooper (member 1523)

only think of clouds as the opposite of fine weather. A lazy sunny afternoon beneath the drifting candyfloss curls of the Cumulus is far finer than the flat monotony of a cloudless sky. Don't be brainwashed by the Sun fascists – fair-weather Cumulus have a starring role in the perfect summer's day.

Candyfloss clouds

There is one other species of this cloud: Cumulus fractus. This has a much less puffy shape, its edges being fainter and more ragged. It is the way a Cumulus looks when it is decaying at the ripe old age of ten minutes or so.

Besides being divided into species, each of the ten main cloud types – each 'genus' of cloud – has a number of possible 'varieties'. These are characteristics of appearance that are often observed in that cloud type. For the Cumulus cloud, the only recognised variety is Cumulus radiatus, which is when the clouds are lined up in files parallel to the wind. These rows of cotton wool tufts are sometimes called 'cloud streets'.

Although Cumulus is generally associated with fine weather, any cloud can under certain conditions develop into a rain-bearing formation, and Cumulus is no exception. The innocuous Cumulus humilis and mediocris can on occasions grow into the angry, towering Cumulus congestus, which it must be said is anything but a fair-weather cloud. It is well on the way to becoming the enormous awe-inspiring Cumulonimbus thundercloud, and can itself produce moderate to heavy showers. Whilst the development of Cumulus clouds from humilis right up to the congestus and beyond can be a daily occurrence in the hot, humid tropics, it is less common in temperate climes. Nevertheless, if you see Cumulus develop into the tall congestus stage before midday, there is a distinct possibility of heavy showers by the afternoon. Attention all cloudspotters: 'In the morning mountains, in the afternoon fountains.'

THE DISTINCTIVE SHAPES of Cumulus clouds may go some way to explaining why they are the cloud of choice in the drawings of young children. No six-year-old's picture of a family in front of

HOW TO SPOT

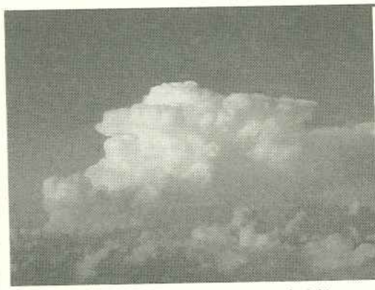
CUMULONIMBUS CLOUDS

Cumulonimbus are thunderstorm clouds, characterised by their enormous height. They are typically tall enough to reach the top of the troposphere, where they spread out in plumes of ice particles that can appear smooth, fibrous or striated. They have dark bases and produce heavy showers – often of hail – which can be accompanied by thunder and lightning.

TYPICAL ALTITUDES*:
2,000–45,000ft

WHERE THEY FORM:
Common in tropical and temperate regions. Rare in polar ones.

PRECIPITATION (REACHING GROUND):
Heavy downpours, often of hail.

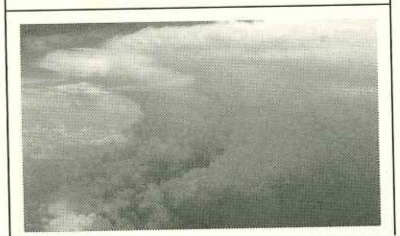


Cumulonimbus calvus (means 'bald')

Cumulonimbus capillatus (means 'hairy')

CUMULONIMBUS SPECIES:
The two species are distinguished by the appearance of the cloud's top.
CALVUS: When the upper region is of soft indistinct flattened mounds, without any fibrous or striated appearance.
CAPILLATUS: When the upper region is cirrus-like and fibrous or striated, often in the shape of an anvil, plume or a disorderly mass of white hair.

CUMULONIMBUS VARIETIES:
There are no official varieties.



NOT TO BE CONFUSED WITH...
NIMBOSTRATUS: which is a dark, ragged precipitating layer, covering the sky. It can look similar to a Cumulonimbus that is directly overhead (and also appears to cover much of the sky) but the precipitation will tend to be more steady and more persistent than the short heavy showers of the Cumulonimbus. If thunder, lightning or hail is present, then the cloud is a Cumulonimbus.
CUMULUS CONGESTUS: from which a Cumulonimbus often develops. Seen from a distance, the cloud is said to have changed into a Cumulonimbus when parts of its upper region begin to lose their sharp edges, due to the droplets freezing into ice crystals. Thunder, lightning or hail will also identify the Cumulonimbus.

* These approximate altitudes (above the surface) are for mid-latitude regions.

Top left: Bob Jagendorf (member 1480). Top right: Mike Davies (member 1633)
Bottom: Paul Cooper (member 1523)

IT IS ALSO A SERIOUS hazard to aircraft. This cloud's hail can grow large enough to severely damage a plane's fuselage, and its lightning can take out the electrics. The supercooled water droplets that form in the cloud's upper reaches can coat a plane's wings with ice, fatally altering its aerodynamics and – most dangerous of all – the enormous, turbulent air currents within its central tower can flip an aircraft over like a pancake.

No wonder pilots do all they can to avoid flying too close to these storm clouds. If they can't pass around one, and their plane is capable of flying at high altitudes, they will generally climb over the top. And that is exactly what Lieutenant-Colonel William Rankin, a pilot in the US Air Force, was attempting to do in the summer of 1959 when his jet fighter's engine seized completely and he had to eject. He became the only man to fall through the heart of the King of Clouds and live to tell the horrific tale. His experience made him something of an international celebrity.

Rankin was on a 70-minute routine navigational flight from the South Weymouth Naval Air Station in Massachusetts to his squadron's headquarters in Beaufort, North Carolina. Before take-off, he'd had a word with the meteorologist at the air base, who'd told him to expect isolated thunderstorms *en route*. The thunder-clouds could be expected to reach altitudes of 30,000 to 40,000ft. For a decorated Second World War and Korean War vet like Rankin, this was fairly routine stuff. He knew his jet could reach 50,000ft comfortably and so he was confident of being able to fly over any storms without difficulty. That, of course, was assuming the engine wouldn't conk out just as he was above one.

Forty minutes into the flight, as he was approaching Norfolk, Virginia, Rankin spotted the distinctive shape of a Cumulonimbus ahead. A storm was raging in the town below and the cloud rose in an enormous tower of puffy convection mounds, mushrooming out into a broad, wispy canopy at its top. The summit was at around 45,000ft – somewhat higher than he'd been led to expect by the official back at South Weymouth – so the pilot began a climb to 48,000ft to be sure of clearing it.

Lt.-Col. William Rankin – before he got intimate with a Cumulonimbus.

Rankin was directly over the top, at an altitude of 47,000ft and a speed of mach 0.82, when he heard a loud bump and rumble from the engine behind him. He watched in disbelief as the rpm indicator on his dashboard spiralled to zero in a matter of seconds and the bright red 'FIRE' light began flashing urgently.

Sudden and unexplained engine seizure like this is a one-in-a-million kind of emergency and Rankin knew that he would have to act fast. Without power, the jet's controls became ineffective and he instinctively reached for the lever that deployed the auxiliary power package to restore emergency electricity. As he pulled the lever, however, he was horrified to feel it come away in his hands. This sounds like a moment worthy of Buster Keaton, but Rankin was finding it anything but funny. He was wearing just a lightweight summer flying suit. It was unheard-of to eject at this altitude at the best of times. To do so without a pressure suit would surely be suicide.

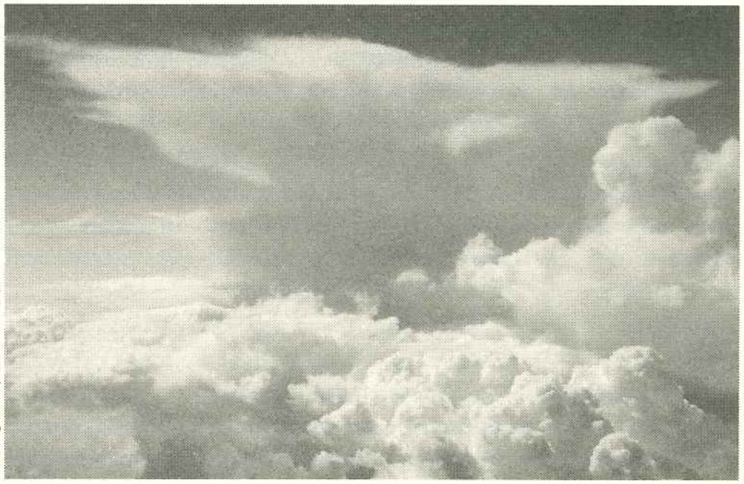
'The temperature outside was close to –50°C,' Rankin later recounted. 'Perhaps I would survive frostbite without permanent injury, but what about "explosive" decompression at almost ten miles up? And what about that thunderstorm directly below me? If it could be hazardous for an aeroplane in flight, what would it do to a mere human?'[1]

There was little time to ponder the dangers. In a matter of seconds, Rankin realised he had no option but to reach behind his head and yank with all his might on the ejection seat handles. At almost exactly 6pm, he exploded out of the cockpit and began his descent towards the cloud below.

IT IS ESTIMATED that some forty thousand thunderstorms occur around the world each day. At the heart of every one is a Cumulonimbus cloud – often many of them. The cloud can be thought of as Cumulus with ambitions to take over the world. It is what results when a humble convection cloud grows vertically through the mediocris and congestus stages and refuses to stop. A Cumulonimbus can develop from other cloud types too, but does so most commonly from a power-crazed Cumulus like this.

A Cumulus, but turned up to eleven

The classic shape of a mature Cumulonimbus is a huge vertical column, several miles across and extending up as high as 60,000ft (over 11 miles), which spreads out at the top to resemble a blacksmith's anvil. This upper canopy is called the 'incus' (after the Latin for anvil) and consists of ice crystals, rather than the water droplets that make up the rest of the thundercloud. The anvil can stretch out over hundreds of miles, as it is spread by the strong winds high in the atmosphere. From a distance it can have a calm, majestic beauty.



Nick Lightbody (member 95)

You can't miss a Cumulonimbus incus, with its distinctive anvil-shaped top, called an 'incus'.

'AT FIRST THERE WAS no sensation of falling, only of zooming through the air,' said William Rankin of the moments after he ejected from his stricken jet. Within seconds, he was suffering from the effects of the inhospitable environment at 47,000ft.

'I felt as though I were a chunk of beef being tossed into a cavernous deep freeze,' he remembered. 'Almost instantly all exposed parts of my body – around the face, neck, wrists, hands and ankles – began to sting from the cold.' Even more uncomfortable was the decompression caused by the low pressure at the top of the troposphere as he began the free fall until his parachute would automatically open. He was bleeding from his eyes, ears, nose and mouth as a result of the expansion of his insides, and his body became distended. 'Once I caught a horrified glimpse of my stomach, swollen as though I were in well-advanced pregnancy. I had never known such savage pain.' The one benefit of the extreme cold was that it began to numb his body.

Not the best of flights

In spite of the spinning, flailing nature of his free fall, Rankin managed to secure the emergency oxygen supply to his mouth. It was essential to remain conscious if he was to have any chance of surviving the descent. He was within the upper reaches of the storm cloud, with deteriorating visibility, when he saw on his watch that five minutes had passed since he had ejected. He should have passed the 10,000ft point by now – the height at which the barometric trigger in his parachute would cause it automatically to open. But there was no sign of the parachute. The poor pilot had already suffered an engine failure at 47,000ft, the jet's auxiliary power lever coming off in his hand and having to eject directly over an enormous storm. Now it was beginning to look like he was hurtling through the air strapped to a parachute that didn't work.

Deep within the ice-particle upper region of the Cumulonimbus it was dark with zero visibility. This made Rankin totally disorientated, with no idea of his altitude. For all he knew, without his parachute opening he might hit the ground at any moment. It was therefore with great relief that he felt the violent jolt as his parachute finally deployed.

The tension in the risers was enough to reassure him that it had fully opened. He was also relieved to find that, though his emergency oxygen supply had run out, the air at this level was now dense enough for him to be able to breathe without it. In the gloom of the enormous cloud, things appeared to be looking up: 'Under the circumstances, overjoyed to be alive and going down safely, consciously, even the increasing turbulence of the air meant nothing. It was all over now, I thought, the ordeal had ended.' But the turbulence he was beginning to feel and the freezing hailstones starting to strike him meant that he was only now reaching the heart of the storm.

Ten minutes into his descent, Rankin should have been reaching the ground, but the enormous draughts of air that surged up the core of the cloud were retarding his fall. Soon the turbulence became much more severe. He had no visual point of reference in the gloomy depths but he sensed that, rather than falling, he was being shot upwards with successive violent gusts of rising air – blasts that were becoming increasingly violent. And then for the first time he felt the full force of the cloud.

'It came with incredible suddenness – and fury. It hit me like a tidal wave of air, a massive blast, fired at me with the savagery of a cannon... I went soaring up and up and up as though there would be no end to its force.' Rankin wasn't the only one being hurled up and down. In the darkness around him, hundreds of thousands of hailstones were suffering the same fate. One minute they were falling downwards, dragging air down with them; the next minute, they were swept back up by the enormous convection currents within the cloud.

With this falling and rising, the hailstones picked up freezing water and grew in size, hardening layer by layer like gobstoppers. These rocks of ice pelted Rankin with bruising force. He was now vomiting from the violent spinning and pounding and he shut his eyes, unable to watch the nightmare unfolding. At one point, however, he did open them to find himself looking down a long black tunnel burrowing through the centre of the cloud. 'This was nature's bedlam,' he said, 'an ugly black cage of screaming, violent, fanatical lunatics... beating me with big flat sticks, roaring at me, screeching, trying to crush me or rip me with their hands.' Then the lightning and thunder began.

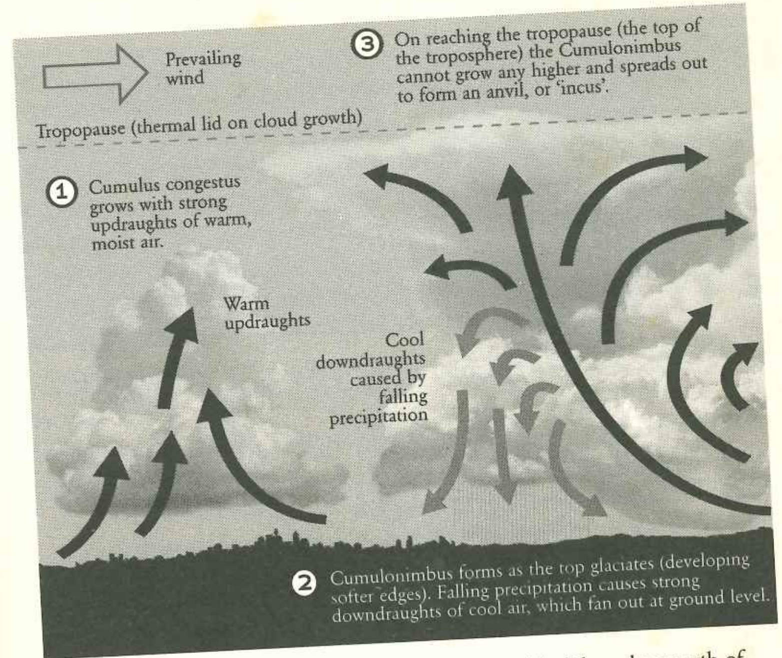
The lightning appeared as huge, blue blades, several feet thick, which felt as though they were slicing him in two. The booming claps of thunder, caused by the explosive expansion of the air as the enormous electrical charge passed through, were so over-powering up close that they were more like physical impacts than noises. 'I didn't *hear* the thunder,' he said, 'I *felt* it.' Sometimes he had to hold his breath to avoid drowning from the dense torrents of freezing rain. At one point he looked up just as a bolt of lightning passed behind his parachute. It lit up the canvas, which appeared to the exhausted pilot as an enormous, white-domed cathedral. As the image lingered above him, he thought that he had finally died.

How it feels to be a hailstone

THREE CRITICAL CONDITIONS of the atmosphere provide an ideal environment for a fledgling Cumulonimbus cloud to grow into a large, angry specimen:

1) There needs to be a ready supply of warm, moist air around the cloud. This acts as the energy source, fuelling the cloud's growth. The central core contains enormous updraughts of air, rising at speeds of 25–70mph, and the stream of air that supplies this updraught is known as the 'inflow'. When the inflow air is warm and moist, plenty of heat is released as it forms water droplets within the cloud. This energy gives the air at the centre buoyancy, increasing the updraughts and the cloud's growth.

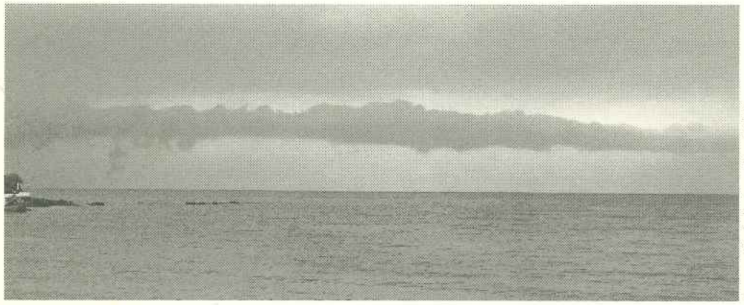
2) The tropospheric winds around the Cumulonimbus need to increase considerably with height in the direction of the cloud's movement so as to encourage it to slant forward. This is critical for the cloud's longevity because its central tower is not just the region of violent updraughts; it is also the part where the heavy precipitation, such as hail, develops. As the precipitation falls through the cloud it can chill the air by partly evaporating and in addition drags the air down with it. The plunging downdraught so formed can, if the cloud is vertical, swamp the life-giving



The top of the troposphere, which acts as an invisible lid on the growth of clouds, is what causes the Cumulonimbus to spread out in an anvil shape.

updraught to kill off the cloud quite quickly. These downdraughts reach the surface to spread out like water poured on a table – often causing an advancing line of low cloud at the leading edge. However, when the surrounding winds make the Cumulonimbus slant forward, the precipitation falls slightly ahead of the updraught, reducing its tendency to cancel out the rising core and thereby kill the cloud's growth.

3) The atmosphere around the cloud needs to be 'unstable'. This has to do with the degree to which the air becomes colder with altitude. If the temperature of the surrounding environment decreases steeply with height, then the warm, moist air entering at the inflow and cooling as it rises will always be a little warmer than the air around and so will remain buoyant. This is what encourages the growth of the cloud. The troposphere always tends to become cooler with altitude, but it often does so more dramatically near the



A 'roll cloud' can sometimes appear in advance of a storm. It forms as the cool downdraughts spread out at ground level and push up the warmer air ahead.

surface in tropical regions where the warmer ground increases low-level air temperatures. This is one reason why thunderclouds are so common in these parts of the world.

Incidentally, it is the way that the air temperature changes with altitude that gives the Cumulonimbus its distinctive anvil shape. The top of the troposphere is defined as the part of the atmosphere where the air always stops cooling with height. Known as the 'tropopause', it is a layer where the temperature remains constant – say, at around –50°C – before starting to increase again in the lower stratosphere. This change in the temperature gradient acts as a thermal ceiling to cloud growth. A Cumulonimbus reaching it is unable to grow any taller and so spreads out under the ceiling.

Just as Cumulus clouds can occur in the different species of humilis, mediocris, congestus and fractus, the Cumulonimbus can be one of two possible species. These are called 'calvus' and 'capillatus' and they are distinguished by the appearance of the upper, ice-particle region. Cumulonimbus calvus is when the cloud's anvil is smooth with soft edges. Cumulonimbus capillatus is characterised by an upper region that is fibrous and striated. It is named after the Latin for hair, and can look like the disorderly locks of a child who's just been in a playground scrap.

It should come as no surprise that the King of Clouds prefers not to travel alone. Besides the incus anvil at its top, the Cumulonimbus has a whole court of 'accessory clouds' (clouds that only ever appear near or merged with one of the ten genera)

and 'supplementary features' (various forms and protuberances attached to one of the cloud genera). These act like an entourage.

The wide, trunk-like 'wall cloud' is one that forms below the Cumulonimbus base, around the core of its updraught region. 'Pannus' are dark, ragged shreds of cloud that appear below the storm cloud's base, as the air becomes saturated from the heavy precipitation. Ahead of the storm, riding on the front of the outflow of cool air, there can appear a dense shelf or roll of advancing cloud, called an 'arcus'. The 'pileus' cloud is one that can appear as a smooth veil or cap over the Cumulonimbus's summit. It forms when a high layer of moist air is forced upwards by the rising central tower and rarely lasts long before the Cumulonimbus grows through it and it becomes subsumed into the body of the main cloud. The 'velum' forms in a similar way, but is a large, flat patch of soft-looking cloud, which forms when a series of towers from separate clouds act together to push a large region of moist air upwards. The velum can hang around for some time after the Cumulonimbus clouds have dissipated away. Then there is the 'tuba', which is the first sign of a tornado developing below the Cumulonimbus. It is a finger of cloud that lowers from the cloud base, forming in the centre of a vortex, and results from the cooling of the air in the lowered pressure of the spin.

Most dramatic of all the court attendants are the breast-like 'mamma' (which are sometimes called 'mammatus'). These are udders of cloud that can hang on the underside of the Cumulonimbus's anvil and indicate high instability in the air around the top of the cloud. They are associated with particularly violent storms. Finally, there is often a line of growing Cumulus congestus, queuing up along the storm cloud's inflow. These are the pretenders to the throne – ready to step in and assume rule the moment the king expires.

Amidst the mêlée of its fussing court, the Cumulonimbus itself is possessed by an all-consuming fury, which is fuelled by the unstable atmosphere of its reign. How fitting that the events of Shakespeare's *King Lear* should unfold against the backdrop of a raging tempest, for Lear was driven mad by his own unstable atmosphere.

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AERIAL PLANKTON AND ITS CONDITIONS OF LIFE

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CONTENTS

I. INTRODUCTION

Organisms measuring more than a few millimetres in length have distributional areas which are always clearly circumscribed from the geographical point of view. The cause of this, as a rule, is historical: a particular species had possibilities in a previous epoch of spreading between the areas now isolated from one another. Thus most of the larger Swedish terrestrial animals arrived in Sweden during the *Ancylus* period, seven to nine thousand years ago, when a land bridge over the Danish islands united Sweden to north-west Germany. In a similar way the Caspian Sea probably received part of its marine fauna during a certain part of the Quaternary period, when this sea communicated with the North Polar basin. Evidently the cause of this geographically well-circumscribed distribution of larger organisms is due to barriers which cannot be surmounted under usual conditions. This does not always mean that the particular organisms are unable to thrive in areas from which they are now absent. Plants and animals introduced by human agency have in some cases easily adapted themselves to new surroundings and increased with explosive rapidity, as for instance the sparrow in North America, the rabbit in Australia, the mitten crab (*Eriocheir sinensis*) in the rivers of western Germany, or the Canadian pond weed (*Elodea canadensis*) in Europe.

Turning, on the other hand, to small forms and micro-organisms below a few millimetres in length, detailed investigations have shown that distributional limits of the type mentioned above for the larger forms are of much less importance or do not exist at all (Gislén, 1940). In fact, their distribution tends to be more or less cosmopolitan. It is true that they are often restricted to a certain climatic belt, and within this they are as a rule strictly bound to certain ecological surroundings corresponding to their needs. But where these needs are realized—and this can be the case in a vast number of places, as their demands for living space are very restricted—they appear everywhere on the globe, if only the time factor has been adequate. This applies both to terrestrial and aquatic organisms.

Such a cosmopolitan distribution is perhaps not so remarkable in the case of small marine organisms, where currents facilitate a wide distribution of the planktonic larval forms. Quite recently, geologically speaking, there was a free communication around the globe between the various tropical oceans, thanks to the circumtropical Tethys Sea. In this way there was until the middle part of the Tertiary period a rather uniform tropical marine fauna and flora. Since the separation of the oceans at about the end of Miocene times different parallel forms have, in most cases, developed in the various seas. There are forms, however, especially among planktonic but even among benthic animals, which still retain their specific identity on both sides of continental or oceanic barriers, in this way demonstrating the very slow rate of evolution of marine organisms (Gislén, 1944).

Marine forms, especially planktonic ones, have possibilities of spreading in a vast, more or less uniform medium. Because of this and of their conservatism in evolution they are widely distributed. Entirely different problems appear when we turn to terrestrial or limnetic organisms. Fresh-water forms can only spread directly as far as the limits of the water system in which they occur. Terrestrial forms may be impeded in their distribution by water, mountain ranges or deserts, all of which provide barriers which may be totally impassable to larger forms.

As mentioned above, these obstacles are absent in the case of small organisms. For these the only limiting boundaries are climatic and edaphic. Therefore, wherever surroundings are suitable the most astonishing finds can be made of forms which may have been described earlier in far away places on the globe. Thus, among the Mycetozoa several species have been reported partly from Europe and North America, partly from South Africa and South Australia, and there are species known to occur on all five continents. The same is true of the Rhizopoda, Ciliata, Rotatoria, Tardigrada, Cladocera, Apterygota, and others (Gislén, 1940). Similar cases of wide distribution have been recorded for certain algae, fungi and soil bacteria (e.g. Barthel, 1923, p. 60; Lange, 1934).

How are these facts to be explained? It seems as if the increased ability to spread were caused in the first place by the influence of the wind in transporting small objects. But there are other distributional agencies, such, for example, as water or the fur and feathers of large animals.

II. DISTRIBUTION OF LARGE ORGANISMS

Even large forms can be distributed through the air by birds. As a rule it is the reproductive stages alone, but full-grown forms too, such as leeches, are sometimes spread in this way. Neiman (1924) showed that spawn of two species of pond snails could be transported when stuck to a glass plate and hung out of the window of a train during a journey of 30–75 min. without serious reduction in the number of eggs which developed. The older the embryos the better they withstand such transport. Incidentally the experimental conditions in this instance were much less favourable than those in transportation by a bird, as in the latter case there are often protecting hollows or feather-clad areas where organisms carried on the bird can survive more readily. That long distance transport by birds can actually take place is shown by the fact that a duck was shot in the Sahara at least 100 miles from the nearest body of water with fresh mollusc spawn attached to one of its feet (Weber, 1914, p. 520).

Water currents may also be important. Palmén (1944) has found that insect species new to Finland are often driven ashore in a living state on the southern coast of that country. In this case, however, the animals, often in an exhausted condition, reach a shore which is unsuited to their mode of life. They therefore usually perish before reaching localities where they could survive and propagate. In spite, therefore, of living specimens of new species being driven ashore every year, these do not become indigenous.

As regards distribution by air, there was considerable early speculation. Only recently, however, has it been possible to obtain a tolerably correct conception of the appearance and frequency of the organisms present in the air. It is now certain, however, that the air harbours an invasion army, rich in small animals, plant-spores and so on, which are constantly recruited from the earth's surface. These form the plankton of the air.

In our latitudes violent winds are infrequent, but there exist, for instance on hot days, strong upward thermal convection currents. From measurements carried out by aeroplanes it is known that these upward currents can reach altitudes of at least 1000–1500 m.; they are generally not strong above 300 m. At night the air cools down, especially near the earth's surface, and especially in the lower air layers. There is then a tendency to develop downward currents. The higher layers of air are cooled more slowly than those near the ground and will, therefore, be a little warmer at night. Upward currents are also produced when a horizontal wind meets a mountain range. The wind passes over the range, often with great velocity, and then diminishes in force. By different degrees of heating of the air, for instance over land and over water, differences are produced in the upward currents within a given area. Clouds too play an important part in the intensity of upward movements of the air. Over smaller heated areas air pockets may be found. Strong air currents also appear around a storm centre and in connexion with heavy rains.

In hotter countries the air may, on certain occasions, be subjected to exceptionally violent movements. Tornadoes and typhoons at their maximum strength can produce a wind velocity estimated to be about 100–250 m./sec. With such a velocity the tempest can carry with it all that comes in its way. McAtee (1917) made an inventory of some singular cases. Thus an iron screw weighing 338 kg. was hurled 270 m., a chicken coop of 4 × 4 ft. and a weight of 38 kg. was transported a distance of 7 km., a tin roof went 25 km., and a church spire 28 km., before reaching terra firma again.

A spout formed by a tornado has the power of sucking up water. In this way small fishes, invertebrates, and small loose plants will make an occasional journey through the air before they reach the earth's surface anew. These so-called rains of fishes have most often been reported from India and have been witnessed by scientists. Gudger (1921, 1929) related a number of interesting cases. De Castelnau (1861) reported from Singapore that he found masses of the fish *Clarias batrachus* in his garden after an exceptionally heavy rainstorm. In Katywar there was a colossal downpour of rain in the year 1850; in only 90 min. 185 mm. of rain were registered, and in this time so many fish fell from the air that the earth was literally covered with them. Rains of fish have also been reported from more temperate zones, namely New York, Holland, the surroundings of Paris, and Great Britain. In Scotland small herring rained down 3 miles from the sea coast. Further data are given in the papers of Gudger referred to above. Fishes transported through the air rarely measure more than 5–10 cm. in length, but some are up to 15 cm. (exceptionally 30 cm.). Sometimes the upward, often very humid, air currents rise to such altitudes that the moisture carried with them may freeze and be precipitated in the form of great hailstones. In exceptional cases small frozen fishes have been found inside these hailstones, and in one case, in America, even a small turtle.

An important fact is that in several of the cases mentioned the transported animals were still alive. Prévost threw small living fish from the roof of a house 30 m. high down on to wet mud and found that they survived. The experiments were continued by dropping small trout from an aeroplane on to frames with netting floating in a lake. The fish could thus be recaptured and it was found that all of those that had fallen within the frames were in good condition, provided only that they were less than 7·5–12·5 cm. in length. With this small size the resistance of the air is so large relative to the weight of the falling body that a constant, rather moderate velocity is acquired which does not endanger the life of the animal when it hits the water. The trout was generally dropped from a height of 100 m., but above an altitude of 25 m. the speed of falling was in fact not increased. The method has been used in Canada to implant trout in lakes which have been devoid of fishes since the Glacial Period (Prévost, 1935, and in a letter; Prévost & Piche, 1939; Darlington, 1938*a*, p. 282).

Although wind may transport even vertebrate animals through the air, yet this method probably does not play a large part in the distribution of these animals. Nevertheless, Gulick considers (1932) that the absence of salamanders, frogs, larger molluscs, and mammals on an island is evidence against a land bridge to the island. Darlington (1938*a*, p. 283) has pointed out the possibility of an aerial dispersal of even relatively large animals by huge palm-leaves, in the rolled basal parts of which they may be transported safely during hurricanes.

III. DISTRIBUTION OF SMALL ORGANISMS

The presence of small molluscs on an island might be explained through transport by birds or by wind, for if there had been a former land bridge a larger part of the fauna of nearby areas should also have invaded the island. The fauna of many oceanic islands seems to be composed by mere chance. Darlington (1938*b*), who investigated carabid beetles occurring on Mediterranean and West Indian islands, states that they are all small and are probably driven by weather from nearby continents. By means of hurricanes, for instance along the chain of the Antilles, the aerial transport of small forms might be expected to occur regularly. But weaker wind currents may also act as dispersers. Regular migrations of insects are known from North America. In the spring they come northwards with northerly winds, in the autumn southwards with southerly winds. Gypsy moth larvae have been shown to be transported by wind for distances of 32–50 km. (Collins, 1917).

Investigations have been carried out with catching apparatus, transported in the air and exposed at a certain height, later to be closed before return to the ground. Such experiments have been made both with kites (Hardy & Milne, 1937, 1938) and from aeroplanes. These investigations were begun during the 'twenties, and preliminary results were published in the beginning of the 'thirties by Coad (1931) and Berland (1935). In 1939 Glick published a comprehensive paper on the subject in which he analysed the results obtained by an examination of his large amount of material. In these investigations it was shown that up to considerable heights there exists an important aerial plankton. Berland investigated the air up to 2300 m. in the vicinity of Paris. Glick reported flights carried out in Louisiana between altitudes of 6 and 4500 metres throughout a year both by day and by night. During 1000 flying hours 30,000 animals were captured. In order to obtain comparable results the catching apparatus was always exposed during a flying time of 10 min. The maximum quantity of air plankton was obtained in May, the minimum in December and January. During calm days more insects were obtained at 60 m. than during windy ones; during days characterized by agitated air masses there was an increase in the layers between 300 and 1500 m. By night a somewhat larger number of animals was obtained below 600 m. than during the daytime, but higher up there was scarcely any difference. On moonlight nights rather more insects were in the air than on dark nights. With strong upward currents small animals were carried to heights of 900–1200 m. in a day. The greatest number of insects in the air was found when the sky was partially cloudy and consequently much turbulence prevailed in the atmosphere. With heavy rains and a low temperature few insects were found in the air. After rains, thanks to rising temperatures, there was much aerial plankton.

Diptera were found to be commonest; they were followed in frequency by the Coleoptera, especially Carabidae and Staphylinidae. The insects were most abundant near the ground. At a height of 60 m. the density of the population was only half of that at 6 m. At 60 m. on an average 13 specimens were obtained per 10 min. flying time; at 300 m. this figure had been reduced to 4·7. At 600 m. the number had been halved, and at 900 m. the population density was half of that at 600 m. From 900 up to 4200 m. the quantity was roughly the same. Large and strong flying insects were obtained at lower altitudes, rarely over 900 m. At higher levels the animals scarcely ever exceeded a length of 3–4 mm. (Berland, 1935, p. 90). Within any group of flying insects the smallest were always obtained at the greatest heights; often, however, they had large floating structures. Several Homoptera, Hymenoptera and Diptera were collected up to a height of 4200 m. Many absolutely wingless forms were also taken at high altitudes, and gossamer occurred up to 3300 m., one spider being even found at 4500 m. Mites and wingless ants occurred at 900 and 1200 m., and a flea was taken at 60 m. The air plankton at greater heights consists mostly of small flies, mosquitoes, small Coleoptera and Heteroptera, Homoptera, parasitic Hymenoptera, and small spiders. It has been calculated that an air column with a height of 4200 m. and a cross-section of a square mile generally harbours about 25 millions of such small animals (Hardy & Milne, 1938).

The strongly flying insects, which are found at low levels, distribute themselves chiefly by their own power of flight, while smaller forms are often swept into the upward currents and are then distributed passively. Small spiders, for example Linyphiidae, have made this wind transport their normal type of distribution. In fine late summer weather with weak air currents they spin a long thread from some elevated position; the wind seizes it, and, attached to the thread, they float up into the air.

When a storm is approaching, animals often become agitated and uneasy. With this type of weather strong gusts of wind or whirlwinds occur, which carry up small particles and small animals from the ground. A proof that most animal forms which appear at high levels in the air consist of individuals often carried from elsewhere was given during the great Mississippi flood of 1927. In flights at a height of 60 m., eight times as many individuals were found in the air plankton over the non-flooded areas than over the flooded territory. On the other hand, at an altitude of 300–1500 m. this difference disappeared and the same number of animals was obtained over land and water; the air plankton had evidently been blown in over the flooded areas.

During the journey of animals upwards through the air their existence is endangered by drought, frost, low air pressure and strong solar radiation. Many individuals die, but there are numerous cases showing that they can survive journeys at considerable altitudes and of long duration.

Hardy & Milne (1937) captured several hundred insects by kites sent up to a height of 60–120 m. over the North Sea, 200–250 km. away from the nearest land. At 215 km. off the west coast of Africa the *Discovery* was invaded by numerous moths and countless grasshoppers, locusts and flying bugs. The same vessel, 515 km. off Portugal and 570 km. off Morocco, was boarded by sphingids and even a butterfly. The large American monarch butterfly (*Danaus plexippus*), famous for its migrations from North to South America, has also been found occasionally in Ireland, England and Portugal, and even in the Southern Pacific, 830 km. from the nearest land (Williams, 1930). A swarm of migratory locusts boarded a vessel between Bordeaux and Boston, 2500 km. from the nearest land (Glick, 1939). All the insects mentioned here are larger forms which can fly far from land by their own wing-power. The wind also plays a certain part, as is shown by the devastating swarms of migratory grasshoppers which often accompany special winds and disappear when these change.

The occurrence of small forms in the catches shows that these can endure long air journeys, having been passively transported. A large number of the animal forms found in aeroplane traps are still alive when taken out. Living insects have been collected in traps after flights from 60 up to 2700 m. The following case is probably the most remarkable example of the air transport of small animals for a long distance. An expedition sent out from Oxford to Spitsbergen reported that on 8 August 1924, after a strong southerly gale, the snowfields and glaciers of North-East Land were studded with various insects, chiefly aphids. About 80% of those collected were still alive. The plant lice turned out to be *Dilachnus piceae* parasitizing the spruce. The nearest locality for spruce is on the Kola Peninsula, situated at almost 1400 km. from North-East Land* (Elton, 1925, p. 291).

It might be thought that wind would be a considerable danger to animals transported by air. A strong wind has great powers of rapid drying. Normally the velocity of the wind at a height of 1800 m. is probably more than 25 km./hr. In several cases insects have been taken in aeroplane traps at great heights, when the wind velocity was 75 km./hr. With such a velocity the transport from the Kola Peninsula to Spitsbergen would have taken less than 20 hr.; the actual force of the wind on the occasion mentioned suggests something between 12 and 24 hr. (Elton, 1925, p. 294). Floating in the air, however, the insects are not subjected to the desiccating power of the wind, since they have the same velocity. Desiccation only threatens during clear weather, while the risk is not great in a foggy or cloudy atmosphere.

Temperature, at least during the warmer part of the year, is probably not a limiting factor for distribution in the lower layers of the air. The average temperature falls about 1° C. for every 150 m. up, which means that at a temperature of 20° on the ground, freezing-point should be reached at an altitude of about 3000 m.

Air pressure at 5500 m. falls to half of that on the ground to be halved again at double that height; at 20 km. it is about 40 mm. of mercury (Lysgaard, 1943, p. 76). Lutz (1932) placed ten flies in a humid chamber in which the air pressure was lowered to 22 mm. Hg in 90 sec. Four minutes after air at atmospheric pressure had been let in again, all the flies were as active as before the test. After repeating the experiment twenty times only six flies were still alive. These flies, however, gave normal offspring for several generations.

Mr H. Emanuelsson and I have been able to verify the rather startling observations of Lutz. In our experiments, which are not yet finished, we have extended the investigation to include various Diptera, Coleoptera, Lepidoptera, Hymenoptera, Opilionida, Araneida, Chilopoda, Diplopoda, Isopoda, Mollusca and Oligochaeta. Provided that the surroundings were humid, the forms investigated supported

* During the last two decades a new mode of distance distribution has arisen through air transport by man. On the outside of an aeroplane the strong air currents soon sweep away everything. But various organisms may slip in with foodstuffs, vegetables and flowers transported by the plane. In the air ports of North America to-day all material brought in, as well as the interior of the aeroplane, is always searched for foreign insects. In this way, in 1933, insects from Central and South America were obtained in 81 cases. When the airship *Graf Zeppelin* made its first visit to North America in 1928 seven insect species were found in bouquets decorating the cabins; in 1929, on a similar occasion, twenty species were obtained, six of which had never before been taken in North America (Johnston 1934).

a lowering of barometric pressure (in 2–3 min.) to 70–50 mm. Hg before they showed signs of being seriously affected. At that pressure they sometimes defaecated, showed rather rigid movements and often became more or less extended. At a pressure of about 15 mm. most species were lying on their side or back, quite motionless and looking as if dead, but snails and oligochaetes continued to creep, probably because of the insignificant oxygen consumption for the motion of their smooth muscles. Generally the animals were kept at the low pressure mentioned for 2–3 min., after which normal pressure was restored in 1 min. Isopods, chilopods, diplopods and most spiders then began to move almost immediately, while it generally took the insects 1–3 min. before they walked and flew again. In double this time they were behaving quite normally. From this it is clear that land invertebrates have an astonishing power of sustaining and surviving low air pressures.

Back & Cotton (1926) made some experiments at low air pressures to investigate the possibility of using a vacuum as a control of insect pests. At a very low air pressure, between 8 and 33 mm., most insects succumbed in less than 7 hr. In two species, however, a small percentage of eggs and larvae were still alive after 24 hr. With a pressure varying between 10 and 85 mm. most individuals were killed in 24 hr., but a small number of eggs and larvae survived for 2 days. When the pressure was kept between 40 and 140 mm. most insects were dead after 3 days. In a few species, however, a small percentage of larvae and even adults were still alive after 6–7 days. As no arrangements were made for maintaining the humidity (cf. p. 1039), the death must have been due to desiccation. The authors state, too, that the dead specimens 'were stiff and brittle and appeared to have been thoroughly dried out'.

IV. DISTRIBUTION OF MICRO-ORGANISMS

Organisms of a size near or beneath the limit of observation with the naked eye have still greater possibilities of air transport. In investigating the powers of distribution of these forms it has not been possible to use the same methods as those applied to the larger planktonic organisms of the aerial sea. Pasteur (1860) collected dust with an *aspirateur* in order to investigate the occurrence of micro-organisms in the air. Interesting investigations were carried out by Erdtman (1937) during a journey from Europe to America. The air was on different occasions sucked up by a vacuum cleaner and the number of pollen grains per unit volume was calculated. Over the North Sea 18 pollen grains per 100 cu.m. were obtained; half way between Europe and America the figure sank to 0·7; off Nova Scotia it had increased to 3·5, and near the coast of New England it was 15. For comparison it may be mentioned that the corresponding figure over land amounted to 18,000. Pollen grains of American tree species were identified at 300 km., in some cases even as far as 650 km. from the nearest land, and pollen of some other species was found up to 1000 km. from the coast.

Charles Lindberg, however, was the first person to carry out investigations of microplankton at higher altitudes. In 1933 he flew between America and Europe, and on the way crossed the inland ice of Greenland. On the journey he used an apparatus for catching micro-organisms, the so-called sky-hook. Sterile glass microscope slides were coated in New York with a thin sticky film and were put into a sterilized tube. This was hung out during the flight. Such slides were exposed on various occasions and at different altitudes. The tubes were closed before being hauled in, and were investigated after the return to New York. The flights were carried out over the sea at an altitude of 750–1650 m., and over Greenland at 2400–3700 m. It was found that the glass slides were studded with spores of fungi, unicellular filamentous algae, spicules of sponges, insect wings, volcanic ash, etc. (Meier, 1935).

The peril of drought which threatens larger forms is still greater as organisms approach microscopic dimensions. The ratio of surface to volume increases in smaller forms. This means that such animals, if they are to make use of the possibility of distribution as aerial plankton, must possess qualifications lacking in larger animals. Some of these forms, by passing into a state of lethargy known as anabiosis can endure very considerable losses of water, in fact so great that they shrink to crackling dryness. As soon as they are wetted they imbibe water again, swell out to their original size and shape, become mobile after a quarter of an hour to an hour, and soon creep about as though nothing had happened. Such forms are found, for instance, among the Amoebozoa, among certain Nematoda and Rotatoria, and are especially prominent in the Tardigrada. All these organisms live in situations where drought threatens. Other animals, which do not themselves withstand drying up, or which do not endure transport through the air, have reproductive bodies that are exceedingly resistant.

Both the anabiotic forms and the resistant eggs can endure very long periods of desiccation (Bock, 1936; Lucks, 1929; Wülker, 1926). Eggs of rotifers, after a drought of 13–14 months, developed on being wetted again, regardless of which stage of embryonic development they were in when they dried up. Sars (1886, 1888, 1889) hatched resting eggs of Cladocera, Phyllopoda, Copepoda, and Rotatoria in Norway from mud which had been collected and dried 14–17 months earlier in tropical Australia. Dried bdelloid rotifers have revived on being wetted after 5 years' desiccation. Some species of rotifers have been allowed to freeze and dry seven times successively, after which they were still alive when placed in suitable surroundings. Nematodes living in moss have revived after 10 years' desiccation. The wheat eel-worm, injurious to agriculture, has been shown to live after lying encapsulated in its cocoon in a wheat grain for 27 years. The Phyllopoda, famous for their meteoric appearance in occasional water pools, in which they pass through their development with exceptional rapidity, have drought-resistant eggs. The eggs of many species can endure desiccation for 3–5 years, and some after drying have remained alive for 15 years (Spandl, 1925). By accommodating themselves to temporary pools, and by the exceptional resistance to desiccation of their reproductive stages, these animals have succeeded in occupying a peculiar ecological niche out of danger from modern competitors, and in this way they have been able to survive (Gislén, 1937). Encysted Infusoria may endure years of desiccation; *Peridinium cinctum* has been proved to stand a drought of over 16 years.

Bacteria do not generally withstand more than a few days of dryness. Nevertheless, there are exceptions. Spore-forming bacteria have particular possibilities of surviving in unfavourable surroundings. The malignant anthrax bacillus, which is exceedingly hardy, can remain alive, dried up on a silk thread, for 70 days; its spores can stand drought for years. A rapid drying up, as by a vacuum or in a desiccator, promotes resistance against drought rather than the contrary. The very hardy but not spore-forming *Bacillus pyocyaneus* when dried in air will not live more than 9 days, but it holds out in a vacuum for more than 7 months (Shattock & Dudgeon, 1912).

These animals and micro-organisms, however, are not only very resistant to desiccation but they also endure very varying temperatures. All the organisms mentioned here can endure higher temperatures in dry air than in humid conditions. Dry air will kill bacteria in $1\frac{1}{2}$ hr. at 100° C. Nevertheless, spores will live for 3 hr. at 140° C. Certain multicellular animals which show anabiosis during drought have turned out to be very resistant to heat as well. Dried cysts of *Colpoda* are said to resist dry heat at 100° C. for 3 days (Brues, 1939). Bdelloid rotifers withstand heat of nearly 125° C. At an air humidity of 55–65% all organisms die at 100° C. in less than an hour. At an air humidity of 30% bacteria perish at 70–80° C. in less than 48 hr. Humid warmth kills all spores at 120° in 30 min., and at 140° C. they die in 1 min. (Kolle, Kraus & Uhlenhuth, 1931, p. 854). As a rule, pathogenic bacteria which do not form spores die in a liquid medium at 62° C. Nevertheless, here too there are some more resistant forms. *Bacterium thermophilum* still divides at 63°, but dies in 30 min. at 71°. Certain soil bacteria are still more resistant. Globig (1888, p. 304) found that some of them thrive at 68°, and a micrococcus was observed to divide at 74°. In hot springs a flora especially rich in Cyanophyceae, has been found between 35° and 50°. Above 60° the number of existing forms decreases markedly, from seventeen species to four according to an investigation by Yoneda (1938–40). Out of seventy-seven species in the type of locality mentioned, only five survived over 64°. *Oscillatoria formosa* is known to hold out at 75° while other Cyanophyceae have been found growing at a temperature as high as 85° and bacteria at 88° (Brues, 1939). Hindle (1932) showed that certain amoebae found in thermal waters will stand a temperature of 53–54°. He discusses the experiments of Dallinger and Drysdale, in which by a slow increase of the temperature extended over a period of several years the thermal resistance of certain Protozoa was increased and their descendants were finally able to live at a temperature of 70°. Multicellular animals rarely endure more than 48° in a water medium; their maximum temperature lies at about 51–52°, though in some cases resting stages may tolerate a little more (Brues 1939).

While, therefore, the upper temperature limit that can be withstood by organisms lies tolerably near to their normal temperature, such is not the case for the lower limit, if we consider certain small forms and micro-organisms. Below freezing-point living organisms and their eggs or spores find themselves in dry surroundings, a fact which probably counts in their power of surviving at low temperatures. Staphylococci, which at normal temperatures only live for 5 days, were found to die in an ice box after 100 days, but to be still unchanged in that time at a temperature of −188° C. (liquid air) (Kolle *et al.* 1931). Becquerel (1936) carried out some very interesting experiments to study the capacity of micro-organisms to endure desiccation and cold. Test-tubes containing a little soil were dried in a vacuum over barium hydroxide for 3 months. Some of the tubes were then sealed by melting the open end, while others were closed only by a cotton-wool plug. In the first-mentioned case the air pressure had been lowered to 1/100,000 mm. of mercury. In addition, algae were investigated which had been dried and kept *in vacuo* in tubes sealed 25 years earlier. These tubes were immersed for $7\frac{1}{2}$ hr. in liquid helium and a little later in liquid nitrogen for 20 hr. The organisms had thus been subjected to temperatures of −269° C. and −196° C. respectively. With all possible precautions the contents were taken out of the test-tubes and cultured for some time on a sterilized medium. These algae which had been resting for 25 years, began to grow anew, and from the earth in the other tubes there developed algae, Flagellata, Amoebozoa, Heliozoa, Infusoria, Rotatoria, Tardigrada and Nematoda. These forms had consequently been subjected to drought, very intense cold, and in some cases very low barometric pressure, but in spite of these most unfavourable conditions they had, in anabiotic stages or as spores, been able to survive and to continue their life when the environment again became suitable.

If the distributional barriers encountered by small organisms in the air in the form of drought, cold and a low barometric pressure are not necessarily catastrophic for them, this is not equally true of other environmental factors. Many investigations have shown that the sun's radiation has the power of rapidly killing bacteria and various other micro-organisms. The ultra-violet rays of the spectrum, extending between 400 and 290 mμ are those most biologically active. Most important of these are the so-called Dorno rays (shorter than 320 mμ). According to Coblenz & Fulton (1925) ultra-violet rays seem to be most bactericidal at a wave-length between 280 and 170 mμ. This region of the spectrum is gradually completed at altitudes from 20 to 80 km. The region from 280 to 230 mμ appears soon after 20 km.

Diffuse radiation has less influence on micro-organisms than direct sunlight. According to one investigation tubercle bacilli lived for more than 16 days in diffuse light, but were killed in 6 days by direct sunlight. Placed at a distance of 30 cm. from a 30 amp. ultra-violet lamp tubercle bacilli were killed in 3–6 min. Other investigations indicate still greater sensitivity to sunlight. Bacteria of sputum dried on sand were killed in 10–70 days in diffuse daylight, but in 10 min. to 7 hr. in sunshine; in a humid medium they lived for 6 months. Sensitivity to ultra-violet rays has also been shown for Rhizopoda and Ciliata (Kolle, *et al.* 1931).

The intensity of ultra-violet radiation is very different at different positions of the sun. It is greatest in the middle of a summer day, and decreases rapidly in the morning and afternoon, and also in winter. Götz (1926) found an eight times lower intensity of radiation at midday on 15 December, as compared with the same time on 15 June. In cloudy weather ultra-violet radiation decreases considerably (Lunelund, 1945). In high mountains its intensity increases. Thus at Arosa (1870 m.

above sea-level) it is about twice as powerful as at Schömberg (620 m.) (Jüngling, 1938, Fig. 20). The spectrum at very high altitudes of over 20 km. extends farther towards short wave-lengths and the bactericidal power is correspondingly increased. Cosmic radiation will also play a considerably greater part in higher and more rarified air strata.

Here the question arises as to whether all organisms are influenced unfavourably at higher altitudes by the radiation which they encounter. For forms such as small insects and spiders this is probably not the case. Their air transport is, as shown above, generally carried out at moderate altitudes, under 4000 m., and at these levels the animals were often captured alive. Nevertheless, it might be thought that even if they can endure the radiation themselves their reproductive organs may be injured, thus preventing them from having normal offspring. This, however, is not probable as many small forms have a very wide distribution, which is evidently a result of wind transport. Moreover, a comparatively rich fauna has been found on mountains at high altitudes. Thus Sjöstedt (1910) collected no less than 7000 specimens on the African tropical mountains at altitudes between 1600 and 4000 m., including beetles, flies, grasshoppers, earwigs, Collembola, opilionids, spiders, thrombidiids and other mites, pseudoscorpions and land isopods. On the leaves of the sparse plants small snails (*Vitrina*) with transparent shells were creeping about. However, this belt is as a rule enveloped in a foggy mantle, a circumstance which must considerably decrease the intensity of radiation, and mitigate the violent temperature variations and the evaporation which in this thin air become dangerously strong. On the Himalaya the normal occurrence of plants, in foggy areas, stops abruptly at about 5500 m. (Ruttledge, 1934, p. 308). Animals rarely live higher than 5200 m. Altitudes above 6000 m. are only exceptionally inhabited or visited by living organisms. One Himalayan plant has been found as high as 6400 m. (Smythe, 1932, p. 357). Flying condors may reach heights of 7000 m. and the highest camp of the 1924 Everest expedition, 8200 m., was visited by foraging birds (Hingston 1925). Butterflies and spiders found at very high altitudes (6700 m.) have certainly been blown thither.

When one approaches the dimensions of micro-organisms, however, the sensitivity to radiation seems to change.* As shown above, direct sunlight kills micro-organisms, and especially pathogenic ones, much faster than diffuse daylight. Increased humidity affords a certain amount of protection against sunlight. Consequently micro-organisms floating in fog or in a cloud live longer than those subjected to direct sunlight. At high altitudes, owing to frost and the absence of clouds, floating organisms are subject to considerable desiccation. This desiccation is in itself not directly dangerous, but it makes the micro-organisms more sensitive to the influence of radiation. This has been shown by experiments and is probably due to the sun's rays not being absorbed so much in a dry medium (Wiesner, 1907).

* Spore-forming micro-organisms in particular may under favourable conditions sustain transport at moderate heights, as Proctor (1934) succeeded in growing about 50% of moulds and bacteria collected over 2700 m. and 35% of those collected over 4500 m. All these species, however, were non-pathogenic.

As micro-organisms are especially sensitive to the ultra-violet part of the spectrum, since these rays increase in power at higher altitudes, and since the spectrum in very high layers extends farther towards the short waves which are strongly bactericidal, the sun's rays at high levels become increasingly destructive to micro-organisms. Consequently we can state that while the lower cloudy air strata—let us say under 3000–4000 m.—form a suitable medium for the transport of micro-organisms, the higher layers are very inhospitable to them, not so much because of the low temperature, drought and barometric pressure as because of destructive radiation.

Cosmic radiation hardly plays any part in this connexion. The rather unimportant biological effects which experiments indicate are confined to certain questionable influences on retarded development, accelerated growth of tumours and increased frequency of mutations. It is true, however, that there is a large increase in cosmic radiation at increasing altitudes; it is twelve times more intense at 5000 m. than at the earth's surface, and sixty-three times stronger at 10,000 m. (Eugster & Hess, 1940). Nevertheless, the increase at levels where smaller forms can be transported alive is inconsiderable and, especially when it is a question of transport for short distances at moderate altitudes, should not play any measurable part.

V. DISCUSSION

We may state that large organisms, between a length of a few millimetres and about a decimetre, are rarely transported by the air. When air transport is reported for these forms it is always by means of violent winds or the heavy rains that follow them. Consequently, we can only presuppose a regular wind distribution for them in those rather limited areas where such winds are wont to occur. Nevertheless, one must remember that the cyclonic areas were different in the Glacial Period and that at that epoch an aerial distribution was possible along courses which are now out of the question.

Small forms, that is, organisms varying between a length of a few millimetres to about $\frac{1}{10}$ mm., seem to have great possibilities for distribution through the air by convection winds due to differential heating of the air. Insects and spiders, thanks to their chitinous armour, can, under suitable environmental conditions, survive unharmed in the air for one or several days, and might then again reach terra firma alive (e.g. the aphids in North-East Land). Others cannot survive transport through the air-sea themselves, but have resistant eggs which endure protracted desiccation and which often, besides, are provided with hooks, threads or sticky surfaces, fixing them to leaves or grass blades blown up into the air. In some cases they may be transported attached to flying birds. Some large forms may also be distributed by birds. As a rule it is eggs which are thus carried but even fully grown larger forms such as leeches may use this mode of distribution.

Still other forms, on the border line of micro-size, may have an anabiotic stage during which they are very resistant and can pass unharmed through the air-sea. It is significant that many of these animals are hermaphrodite or parthenogenetic. They have thus freed themselves of the necessity of two sexes and they can therefore produce offspring from a single individual when they come down into suitable surroundings.

Microscopic organisms have a high resistance to unfavourable factors met with during transport through the air-sea. In supporting low temperature, drought and low barometric pressure they are superior to all other forms, and, if the factors mentioned were the only impediments they ought to be able to support transport between different parts of the universe. The dimensions of their reproductive bodies may be so insignificant that they would be driven to other planets or even to stars by radiation pressure. Nevertheless, here time comes in as an important factor in the possibility of transport. In spite of the enormous velocity of a particle impelled through space by radiation pressure it would take 9000 years for it to reach the nearest star. To our nearest planet the time should be only 20 days (Petterson, 1944). A presupposition in such a case would be a starting velocity of several thousand metres per second, a circumstance which seems highly improbable. One must also take into consideration the very unfavourable conditions presented by the ionized strata of the atmosphere (Lysgaard, 1943) where probably all living beings are exterminated.*

Even at the earth's surface micro-organisms are very sensitive to sunlight and especially to ultra-violet radiation. These factors are still more important in the upper layers of the air. Not much is known about the sensitivity of micro-organisms to radiation, but it is evident that while small animals are but little influenced, micro-organisms are much more affected. The eggs of *Artemia* can lie on the edges of desert salt pools in burning sunshine for weeks, months, or even years, without losing their power of hatching, while a micro-organism, or its spores, would long have succumbed. In resting stages such as eggs or other reproductive bodies there are thick protective shells which effectively prevent the entrance of most of the deleterious rays. There is here, moreover, another circumstance which may play a part when micro-organisms are concerned. Since with diminishing size the surface of a body decreases less rapidly than the volume, it follows that with a smaller volume factors acting on the surface become of greater importance. The effect of

* The nitrogen molecules in the F-layer (altitude 180–500 km.) are ionized to N atoms and the oxygen molecules in the E-layer (altitude 90–130 km.) to O atoms by absorbing the very hard ultra-violet rays of a wave-length of over 100 $m\mu$ and about 145 $m\mu$ respectively. Hereby enough heat is produced to exterminate all living organisms (Lysgaard, 1943, pp. 23–25). In this process the ozone, occurring at an altitude of about 25–60 km., and absorbing ultra-violet rays of a wave-length between 145 and 290 $m\mu$ will also contribute (ibid. p. 25). The ultra-violet rays may in addition ionize the organic compounds of the organisms. The question as to whether living organisms, driven forwards through the universe by radiation pressure, can slip in at night on the dark side of the globe is somewhat beyond the scope of this article. Disregarding the role that may be played by the velocity of recombination by night of the N and O atoms (a problem which is as yet not completely solved, according to information given to me by Prof. O. Rydbeck), it seems, however, to be worth while stressing another view-point. In darkness the driving power of radiation is practically lacking and organisms, possibly from another planet, that may have reached the outermost part of the atmosphere sink very little towards the earth's surface at night. When light returns and their velocity towards the earth's surface is speeded up, they are subjected again to the dangerous influence of the ultra-violet radiation and its ionizing effect.

radiation and especially of the chemically important ultra-violet rays, will consequently be greater in micro-organisms. Moreover, the possibility increases of the injurious rays reaching the nucleus thus affecting the cell's vitality. In bacteria there is no real nucleus and damage caused by radiation will probably occur immediately inside the cuticle which may be of a thickness of fractions of a micron. In tardigrades and rotifers the distance to the epithelial nuclei is at least 1μ, while in nematodes with cuticle, subcuticle and deep-lying epithelial nuclei it is much more. Moreover, epithelial cells in multicellular animals are subjected chiefly to one-sided radiation. It is possible that this plays a part in the decreased sensitiveness of organisms to radiation with increasing size. At any rate, the fact is that micro-organisms, in spite of their great resistance to other unfavourable factors met with in the air-sea, soon succumb there on account of radiation. This occurs more rapidly in a dry than in a humid medium, the latter seeming to afford a certain protection against the injurious influence of the rays.

Large quantities of micro-organisms are driven up into the air to return to the ground with downward winds by night, or with showers of rain. The following example shows that large numbers may be involved. Ehrenberg (1849, pp. 286, 291) at Lyons collected dust deposited by the sirocco wind and found 120 species of micro-organisms. They amounted to one-eighth of the whole volume of the dust. The quantity of sirocco dust left by such so-called 'blood rains' has been calculated at between 5½ and 9 tons per square mile. Consequently, almost 1 ton of micro-organisms per square mile may be precipitated on such occasions (Ehrenberg, 1849, p. 310; McAttee, 1917, p. 218).

As small forms and micro-organisms are constantly deposited on the earth's surface one may well ask why they do not flourish everywhere. The answer seems to be that these organisms are often confined to very special conditions of life, or biotopes, and that the smaller the organism, the smaller is also the volume of the biotope. When the small organisms, or their eggs or spores, reach the ground, they will, therefore, in the majority of cases come down in unsuitable surroundings where they must perish. When they happen to meet with suitable conditions it is still not always certain that they will be able to establish themselves there. During those minutes or hours which pass before they have reacquired full vitality, or have reached a reproductive stage, they are menaced by many perils, and it is only after they have surmounted these dangers that the newly started progeny can be considered to have reasonably secured its existence in the biotope.

The number of invaders certainly plays a part here. In the same way that the human body has the power of overcoming a slight invasion of bacteria, nature too, by predatory animals and plankton-catchers which occur in the biotopes, has means by which the balance is maintained within the biotope and by which fresh intruders are as a rule exterminated, if they only appear in small numbers.

Some forms are more exigent than others on a definite type of environment.*

* That some larger forms seem to have lost the capacity of being widely distributed is, as pointed out by Hultén (1937), probably due to the fact that during their past history they have become more

When, however, the requirements of a certain micro-organism are fulfilled, this form will turn up sooner or later, an observation often made by those occupied with such groups (cf. Lucks, 1912). The consequence of this will be that for micro-organisms there are no geographical, but sometimes climatic and almost always edaphic barriers and boundaries, i.e. barriers and boundaries pertaining to the water or substratum in which the organisms live (Gislén, 1940).

These forms are, some of them, cosmopolitan or in other cases distributed around the whole globe within a certain climatic belt. Most of the small forms, and this applies still more to the micro-organisms, are very rigidly restricted to a certain environment. But because of their ease of distribution they occur everywhere, at least within a certain climatic belt, when their needs of definite edaphic factors are fulfilled. This is only so, however, provided that there has been sufficient time for the germs, transported through the air, to get a chance of reaching the suitable locality and of settling there. In other words, small forms and micro-organisms are rarely of biogeographical significance; rather they are representative of a certain type of biotope. Micro-organisms, with the same possibilities of distribution through the air as small forms, are more at the mercy of radiation. Pathogenic bacteria, with their very special demands on environments, are influenced and limited in their distribution by the radiation from the sun. This obstacle is especially active during clear days, while, as shown by the experiments referred to above, these forms will hold out longer in hazy or foggy weather.

Pathogenic micro-organisms and their spores float everywhere in the air. They are hindered in their passage between their different biotope areas by radiation, but even if they land alive on a suitable substratum their vitality, the quantity of infection, and the condition of the host plays a part, for specimens of bacteria of the most dangerous diseases are always found on the mucous membranes even of healthy individual human beings. Under favourable external conditions, especially when ultra-violet radiation is diminished, it is very probable that pathogenic bacteria can also pass through the air from one host to another—perhaps over longer distances than hitherto supposed. In any case it is remarkable that epidemics of the respiratory organs, after raging in foggy, cloudy and stormy seasons, disappear after a period of steady clear weather sets in.

VI. SUMMARY

1. Among animals which can be transported by air currents three main types have been distinguished: (*a*) large forms, from a length of roughly one decimetre down to a few millimetres; (*b*) small forms varying between some millimetres and about $\frac{1}{10}$ mm.; (*c*) animals of a microsize, smaller than $\frac{1}{10}$ mm.

2. Large organisms are usually distributed by wind in typhoon and hurricane areas alone. During the Glacial Period, however, cyclonic disturbances proceeded along other routes, in this way creating distributional paths which are now no longer in use.

and more specialized as regards their environment. During climatic changes they have lost those components of their stock that had the power of surviving in different types of climate. During a warm period the cold-loving forms have been exterminated; in a cold period the warm-loving ones. In this way the species is restricted to a more limited area within which its members can exist.

3. Small organisms have considerable possibilities of distribution by convection air currents and winds at moderate altitudes. Examples are given of such distribution over great distances. But as the animals are often strictly specialized ecologically (herbivores, parasites, etc.) they have particular difficulties to overcome in their new surroundings.

4. Numbers of micro-organisms are constantly being driven up into the air to return again to earth in rain showers or downward air currents.

5. Micro-organisms are very resistant to unfavourable factors met with in the air-sea. Some may be distributed through the air in an anabiotic stage. Being often hermaphrodite or parthenogenetic, many of them can give rise to progeny from a single individual which happens to arrive in suitable surroundings. Their resistance to low temperature, low barometric pressure and drought is superior to that of all other organisms. Nevertheless, in comparison to larger forms, they are very sensitive to radiations, especially ultra-violet, which seem to check their distribution more than that of larger forms.

6. The explanation of the fact that the microforms do not flourish everywhere is found in their very strict biotopical specialization. But wherever a biotope suitable for a certain micro-organism exists, that organism will appear there as soon as sufficient time has elapsed to allow it to be transported through the air and to settle in the locality. The numbers which arrive are a factor in the survival and establishment of the invading species.

7. No geographical borders or barriers exist for microforms. They are often cosmopolitan, or else regionally distributed around the whole globe in certain climatic belts.

8. Under favourable conditions, especially in humid air, the harmful influence of radiation is diminished, and microforms may be transported alive by winds over greater distances than in clear and dry weather.

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