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articles

New evidence regarding the Quaternary geology, archaeology and hominids of Chesowanja, Kenya

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Deposits yielding australopithecines, other fossil mammals and an industry recalling the Oldowan are succeeded by an Acheulian assemblage, overlain by flood plain silts with abundant spreads of later artifacts. The structure is dominated by an asymmetric anticline. Palaeoenvironments are reconstructed and the nature of the raw materials and of the tool makers themselves are briefly discussed.

CHESOWANJA is a Pleistocene fossil and artifact locality in the Northern Rift Valley of Kenya, about 1.5 km west of the track between Mukutan and Tangulbei, at 36° 12' E, 0° 39' N, and 8 km WNW of the point at which the Mukutan river gorge cuts through the Laikipia Escarpment. A diverse fauna includes the partial cranium of a robust australopithecine[1,2].

We report here results from more detailed geological mapping in 1973 and 1974. A remarkable sequence of artifact-bearing levels has been discovered together with a further hominid. The original geological interpretation has been shown to be in error, necessitating re-assessments of the local stratigraphic relationships, the palaeoenvironmental setting and the age of the sequence.

The area is important because the succession of rich artifact assemblages, from a relatively small and well defined region, spans a period probably well in excess of a million years. The associated geology and fossil fauna enable palaeoenvironmental contexts to be inferred for the various phases of hominid activity.

Geological succession

The local sequence of strata (Fig. 1) comprises four lithological units: the Chemoigut Formation, Chesowanja Formation, Karau Formation and Mukutan Beds. Formal descriptions of these and of the geology of the surrounding area will be published elsewhere.

The Chemoigut Formation consists of a sequence of silts and clays with intercalated horizons of coarse tuffaceous and pumiceous sandstone and fine conglomerate. There are calcareous bands and concretions, some of which are of algal origin and thin flaggy and nodular calcrete horizons, several containing abundant root casts. There is also evidence of channelling. The observed thickness of the unit is ~ 25–30 m. The succession overlies red clays containing nodular calcrete, which elsewhere rest on very weathered ankaramitic basalts.

Artifacts have been found eroded out at a number of different sites from at least five horizons. Australopithecine remains come from the two highest levels. The fauna is listed in Table 1.
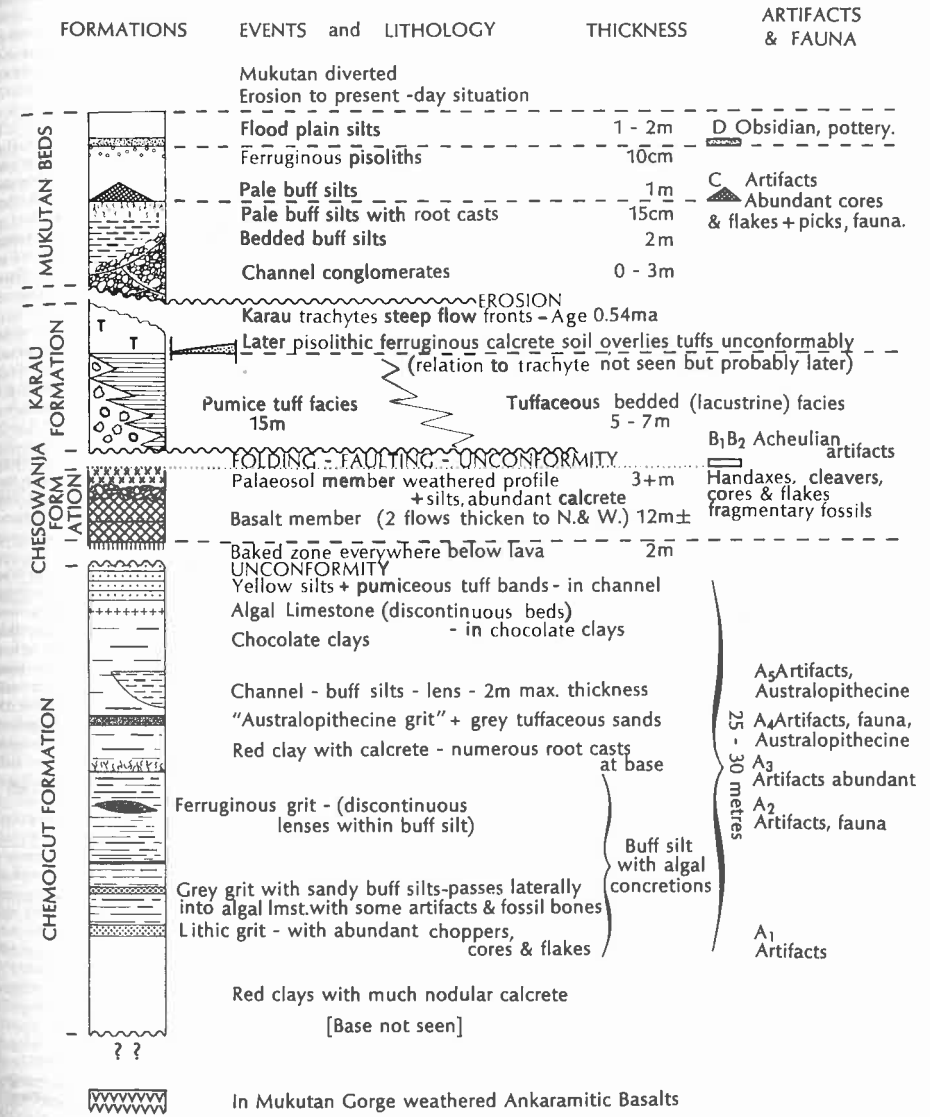
The Chesowanja Formation includes a basalt member composed of two flows, the lower of which is more fissile, and has baked and reddened the upper 2 m of the underlying Chemoigut Formation. It varies from 5 to 10 m in thickness. The upper flow is about 6 m thick. The surface of the upper flow is deeply weathered and large core stones of basalt occur at the base of a palaeosol complex 3 metre thick (palaeosol member, Fig. 1)

containing abundant calcrete concretions. An assemblage of Acheulian artifacts with a sparse but persistent accompaniment of fragmentary fossil material occurs at the upper surface of the formation.

In the west, the lower sediments of the Karau Formation are coarse pumice tuffs about 15 m thick, which lie unconformably over the Chesowanja Formation. The pumice tuffs can be

FORMATIONS		EVENTS and LITHOLOGY	THICKNESS	ARTIFACTS & FAUNA
MUKUTAN BEDS		Mukutan diverted		
		Erosion to present -day situation		
		Flood plain silts	1 - 2m	D Obsidian, pottery.
		Ferruginous pisoliths	10cm	
		Pale buff silts	1m	C Artifacts
		Pale buff silts with root casts	15cm	Abundant cores & flakes + picks, fauna.
		Bedded buff silts	2m	
		Channel conglomerates	0 - 3m	
		EROSION		
KARAU FORMATION		Karau trachytes steep flow fronts – Age 0.54ma		
		Later pisolithic ferruginous calcrete soil overlies tuffs unconformably (relation to trachyte not seen but probably later)		
		Pumice tuff facies 15m	Tuffaceous bedded (lacustrine) facies 5 - 7m	B1B2 Acheulian artifacts
CHESOWANJA FORMATION		FOLDING – FAULTING – UNCONFORMITY		
		Palaeosol member weathered profile + silts, abundant calcrete	3+m	Handaxes, cleavers, cores & flakes fragmentary fossils
		Basalt member (2 flows thicken to N.& W.)	12m±	
		Baked zone everywhere below lava	2m	
		UNCONFORMITY		
CHEMOIGUT FORMATION		Yellow silts + pumiceous tuff bands - in channel		
		Algal Limestone (discontinuous beds)		
		Chocolate clays - in chocolate clays		
		Channel - buff silts - lens - 2m max. thickness		A5 Artifacts, Australopithecine
		"Australopithecine grit" + grey tuffaceous sands		A4 Artifacts, fauna, Australopithecine
		Red clay with calcrete - numerous root casts at base		A3 Artifacts abundant
		Ferruginous grit - (discontinuous lenses within buff silt)		A2 Artifacts, fauna
		Grey grit with sandy buff silts-passes laterally into algal lmst. with some artifacts & fossil bones	Buff silt with algal concretions	
		Lithic grit - with abundant choppers, cores & flakes		A1 Artifacts
		Red clays with much nodular calcrete		
		[Base not seen]		
		In Mukutan Gorge weathered Ankaramitic Basalts		

(note: 25 - 30 metres bracket applies to Chemoigut Formation buff silt with algal concretions)

Fig. 1 Sequence of strata exposed in the Chesowanja area.

equated with 5 to 7 m of fine tuffaceous, well bedded sediments in the east that show graded and current bedding. These seem to represent a penecontemporaneous lacustrine facies of the pumice tuffs. The upper member is the Karau trachyte which exhibits steep flow fronts to the west of the main fossil and artifact localities.

The Karau Formation lies under local unconformities in the vicinity of the artifact and faunal areas; elsewhere it lies under a thin but persistent weathered horizon which has a patchy distribution and is characterised by ferruginous pisoliths. (see Fig. 1).

In the eastern part of the area the Karau formation is overlain by Mukutan Beds, a laterally extensive succession of channel conglomerates and silts approximately 8 m thick. The best exposures are in the Losokweta river valley and along the sides of the abandoned channel of the Mukutan River. Artifacts and fauna occur abundantly along this former course of the Mukutan.

Geometry of the units

The local relationship between the lithological units is shown in Fig. 2. The Chemoigut and Chesowanja Formations are folded into an asymmetric anticline, the axis of which trends north–south. The inclination of the beds on the western limb is about 11°. On the east they are inclined more steeply, and dips in excess of 60° are typical. The characteristically spheroidal weathered top of the upper basalt flow has been seen at only two points.

The Chemoigut sediments are exposed within the core of the anticline structure in three windows, each approximately 200 m across from east to west. The three windows have a total outcrop length of about 1 km from north to south along the main axis of the anticline.

Horizontal strata of the Karau Formation rest unconformably upon the flanks of the anticline indicating post-tectonic deposition. The absence of *in situ* material of this formation resting on Chemoigut sediments suggests that the Karau Formation was deposited before the fold structure in the basalts was breached. The upstanding form of the anticline at that time may account for the differing facies of the rocks on the

east and west of the feature assigned to the tuffaceous member of the Karau Formation.

The more recent Mukutan Beds crop out patchily over an extensive area to the east of the Losokweta River, where they lie under the westerly sloping pediment and wash plain at the foot of the Laikipia Escarpment.

Another hominid

The partial cranium of a robust australopithecine (KNM-CH-1) reported previously[2], came from the unit now called the grey tuffaceous grit within the Chemoigut Formation. More hominid fragments were found in 1973, belonging to another individual (KNM-CH-302). They came from within chocolate clays of the same formation (see Fig. 1) some 3 m higher in the sequence than the original cranial fragment. Although the fragments are surface finds, the local topographic situation (an isolated clay spur yielding fresh artifacts) suggests that they were not far removed from their original position.

The specimens consist of a number of fragments of two molar teeth, probably of the same individual. One is a fragmentary right M[1] or M[2] crown showing features typical of the dentition of robust australopithecines. From the material available it is impossible to ascertain the exact dimensions of the tooth.

Archaeology

Archaeological material comes from at least eight levels within the vertical sequence of some 50 m of sediment and lava already described. All the occurrences are within about 1 km of each other. From their stratigraphic setting the artifacts can be assigned to four age groups, indicated as A_1, A_2, and so on, B, C, and D (Figs 1 and 2).

Group A. These assemblages of cores, chopping tools and flakes without bifaces and cleavers are confined to the Chemoigut Formation. They occur on at least five levels, including those from which the hominid specimens and other mammalian fossils also come. The five artifact-bearing levels have at least ten rich sites from which associations of artifacts are being eroded. No excavations have yet been undertaken but small samples from four of the sites have been collected. The 220 pieces include: 17 choppers; 8 polyhedrons; 4 discoids; 3

protobifaces; 6 scrapers; 5 sundry tools; and 177 samples of waste, debitage, flakes, and so on. In spite of a detailed search no obvious hand axes or cleavers were found within the Chemoigut Formation windows, although they are abundant in group B.

Group B. An Acheulian assemblage with bifaces, cleavers, cores and flakes, comes from the surface of the palaeosol member. The latter is a complex weathering profile developed on the upper flow of the basalt member of the Chesowanja Formation, on the eastern limb of the anticline. At another locality on the same horizon small flakes and cores are dominant. A rather different, younger assemblage of artifacts occurs in association with the weathered horizon containing ferruginous pisoliths.

Group C. A third group of artifacts comprises mainly large cores with piles and spreads of associated flakes, together with occasional bifaces showing an economy of flaking technique, double ended picks, and beaked implements recalling the type 'Sangoan' in morphology[3,4]. Very large local accumulations of this material are found at numerous tool sites along the dry river bed marking the former course of the Mukutan. They are being re-excavated from the pale buff silts comprising the former flood plain of the Mukutan by modern stream action and sheet erosion.

Group D. Obsidian flakes and pottery occur intermingled with debris of group C. They seem to be eroding out from an horizon characterised by the presence of ferruginous pisoliths, stratigraphically a little above the level of assemblage C within the Mukutan Beds.

More recently, the river Mukutan has been diverted for irrigation purposes. Wood from a burnt stump of a large tree along the abandoned channel has yielded a radiocarbon date of 230 ± 110 yr b.p. (unpublished, Birmingham University Radiocarbon Laboratory Date BIRM 537).

Age

In the original publication[2] and in later comments[5,6] it was suggested that the sediments now placed in the Chemoigut Formation were probably younger than 1.2 Myr, but it was stressed that this estimate depended for its accuracy on the geological interpretation. Subsequent work has shown that the relationship of the Chepchuk trachyte (from which the 1.2 Myr date was obtained) to the fossiliferous sediments is not yet established.

The fauna from the Chemoigut Formation (Table 1) is not inconsistent with the original assessment. The *Deinotherium bozasi* Arambourg from the formation would, however, be the youngest known if the K–Ar age of less than 1.2 Myr were accepted. This may prove to be the case, but until additional isotopic dates are available the faunal evidence suggests an age for the formation in excess of 1.34 Myr, which is the date of the latest *D. bozasi* recorded elsewhere (below tuff J, Shungura Formation, Omo[7]).

Palaeomagnetic measurements on material from the baked zone of the Chemoigut sediments lying immediately under the Chesowanja basalt member indicate a reversed polarity (A. Brock, personal communication) and preliminary readings suggest that other levels in the Chemoigut Formation are also reversed (P. Dagley, personal communication). Taking other evidence into consideration, this would place the age of the basalt and the underlying sediments in the Matuyama Reversed Epoch between about 0.7 and 2.4 Myr BP.

The Chesowanja Formation is overlain by the Karau Formation, and a ⁴⁰K–⁴⁰Ar age determination on the Karau trachyte has given a date of 0.54 Myr BP. Micas within the tuffaceous member of the Karau Formation in its lacustrine facies, are also potentially dateable. Preliminary palaeomagnetic measurements of the tuffaceous member have produced a number of normal readings (P. Dagley, personal communication).

Palaeoenvironment

The artifact assemblages of Group A have not yielded examples of hand axes or cleavers. They lie under and predate the typical

Table 1 Fauna from the Chemoigut Formation

Mollusca	
Gastropoda	*Bellamya* sp.
Bivalvia	
Pisces	
Siluriformes	
Reptilia	
Chelonia	
Trionychidae	
Pelomedusidae	
Crocodilia	*Crocodylus niloticus* Laurenti
Mammalia	
Primates	
Cercopithecidae	*Simopithecus* sp. sp. indet
Hominidae	*Australopithecus* sp. (2 individuals)
Proboscidea	
Elephantidae	*Elephas* c.f. *recki* Dietrich
Deinotheriidae	*Deinotherium bozasi* Arambourg
Perissodactyla	
Equidae	*Equus* sp.
Rhinocerotidae	*Ceratotherium* sp.
Artiodactyla	
Suidae	*Mesochoerus* sp. *Metridiochoerus andrewsi Metridiochoerus jacksoni* probably 2 other species
Hippopotamidae	*Hippopotamus* c.f. *amphibius* Linn *Hippopotamus* sp.
Giraffidae	
Bovidae	
Tragelaphini	*Tragelaphus* sp.
? Tragelaphini	
Bovini	
Reduncini	*Kobus* sp.
Alcelaphini	? *Megalotragus kattwinkeli* Schwarz ? *Connochaetes* sp. Small species Smaller species
Antilopini	? *Antidorcas* sp.

Acheulian elements of group B and thus invite comparison with the 'non-biface' Oldowan Industry at Olduvai Gorge. The sediments of the Chemoigut Formation indicate an environment on the margins of a saline lake with a fluctuating water level. Several fresh cores and flakes have a calcium carbonate encrustation of algal origin. It is interesting that the Bed I and lower Bed II Oldowan assemblages of Olduvai also occur around the margins of a saline lake[8].

The Acheulian of group B is from a subaerial environment on the upper surface of a complex weathered profile. The artifact sites lay to the east of an anticlinal ridge at the foot of a pronounced basalt feature caused by the sharp flexure forming the eastern limb. A lake may have existed only a short distance further to the east as the Acheulian surface is overlain by well bedded, tuffaceous strata, indicating deposition in standing water. A sudden local rise in the water level would have occurred with the influx into the catchment area of large amounts of pumiceous ash from the trachyte centre of Karau which lies 4 km to the South-west.

The piles and spreads of artifacts in group C represent stone working sites and occur upon root cast surfaces in flood plain silts. Adjacent fresh flakes can be fitted together on to the large cores from which they were struck. The industry was based on raw material of phonolite cobbles from anastomosing watercourses of the former Mukutan river system. The artifacts were stratified beneath flood plain silts and wash deposits as the local base level rose. Local breaks in sedimentation occur. One of the most pronounced of these is marked by ferruginous pisoliths. Microlithic tools and flakes in obsidian and other lithologies, together with pottery, were stratified during this phase of flood plain deposition which culminated some 2 m above the horizon of group C. Later incision initiated a cycle of erosion which is still continuing and has produced remnant mesas (Fig. 2). This cycle has re-excavated broad channels to below the level of group C and has produced an intermixing,

Fig. 2 Diagrammatic section across the Chesowanja area showing relationships between lithological units (not to scale). (We thank Dr Mary Leakey for the comment that the 'non-biface industry' may prove to be Developed Oldowan.)
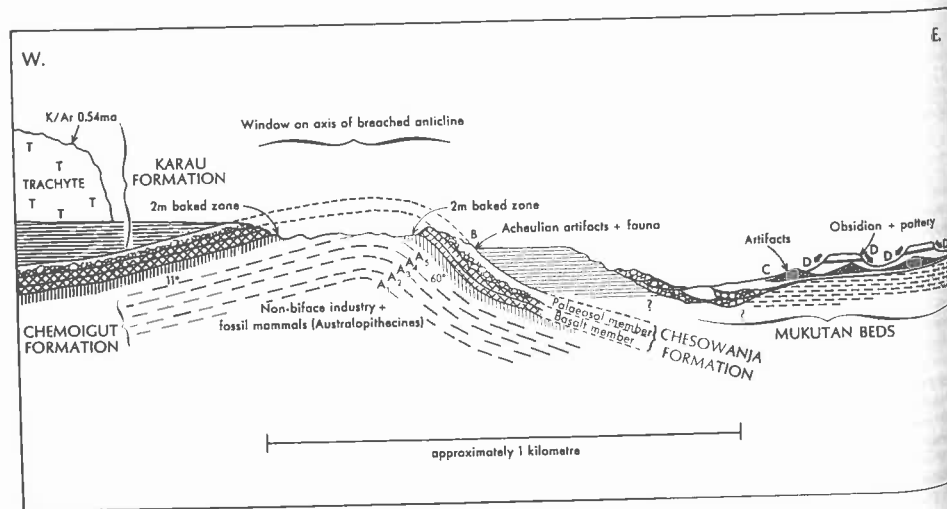
on the present day surface, of elements of groups C and D, together with occasional implements in iron. The exact relationship of these artifacts will only be established by careful excavation of *in situ* material.

The main flow of the Mukutan river was diverted towards the north by the Njemps tribesmen 100 or more years ago to irrigate the wash plain for agriculture.

Raw materials

An ongoing study is concerned with identification of the various rock types used by makers of the tools in groups A–D. The earliest tool kits reveal great petrological variety including different trachytes, phonolites and welded tuffs, together with occasional basalts. The Acheulian raw materials of group B are restricted to trachyte with some phonolite and a few small pieces in welded tuff. Group C is almost entirely based on water rounded blocks and cobbles of phonolite.

Various volcanic rocks occur in the area surrounding the artifact sites. Thus it is possible to carry out petrological and geochemical investigations, including trace element analyses, to identify the source rocks of the artifacts. This will permit an estimate of the minimum ranges over which the early stone technologists travelled to collect their raw materials.

The fact that two more individuals of robust australopithecines have been found from horizons yielding abundant artifacts (others are known from Olduvai Gorge and East

Rudolf), poses the question: "Who made the tools?"

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Significance of autogenously regulated and constitutive synthesis of regulatory proteins in repressible biosynthetic systems

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The functional implications of the different modes of regulation have been examined systematically. The regulatory results lead to certain predictions. The regulatory protein in repressor-controlled systems is constitutively synthesised. In activator-controlled systems synthesis of the regulatory protein is autogenously regulated. There is favourable agreement between these predictions and published experimental evidence.

REGULATION of specific enzyme synthesis has been most thoroughly characterised in the inducible catabolic systems of enteric bacteria[1,2], and in the temperate bacteriophage λ (ref. 3). Regulation of enzyme synthesis in the biosynthetic systems of bacteria has remained more obscure. Among studies on systems of the latter type, those on the tryptophan biosynthetic system in *Escherichia coli* are probably most advanced. Regulation of this operon clearly involves the classical mechanism proposed by Jacob and Monod[4]. Tryptophan, the end product of the pathway, is a corepressor that can combine with an aporepressor molecule to form a "repressor" that binds to the tryptophan operator and blocks transcription[5-10]. Arginine regulation in *E. coli* may also involve a classical aporepressor[11,12], although the evidence is less extensive.

In contrast to the tryptophan and arginine systems, there is no evidence of a classical aporepressor for the histidine and isoleucine-valine biosynthetic systems, although these systems also have been investigated extensively. Consequently, basic assumptions about repressor function have been re-examined critically and other mechanisms have been proposed.

Histidyl-tRNA, rather than histidine itself, has been clearly implicated in repression control of the histidine operon in *Salmonella typhimurium* (see review by Brenner and Ames[13]). Ames and his coworkers[13-15] suggested that a complex of histidyl-tRNA synthetase (aporepressor) and aminoacylated tRNA^His (corepressor) may be a repressor of the histidine operon. In contrast to this suggestion that the synthetase is a negative element in control, Wyche *et al.*[16] reported evidence that the synthetase is a positive element. There is evidence for yet another type of model in which the first enzyme in the histidine biosynthetic pathway (N-1-[5'-phosphoribosyl] adenosine triphosphate : pyrophosphate phosphoribosyltransferase, EC 2.4.2.17) has a role in repression control. Goldberger and coworkers[17-18] proposed that the first enzyme acts as a negative element in the control. But involvement of the first enzyme as a positive element in the control of the histidine operon also has been suggested[18,19].

These and other possible models now can be tested with purified (or partially purified) components in an *in vitro* transcription system and in a coupled transcription-translation system. Blasi *et al.*[21] reported that the first enzyme blocks *in vitro* transcription of the histidine operon but surprisingly, histidyl-tRNA was not required for this result. In contrast, Artz and Broach[22] obtained evidence that a positive element is required for expression of the histidine operon in the coupled transcription–translation system. Their studies also suggest that transcription of the histidine operon requires translation of its specific mRNA. One operon requires translation consistent with these observations. several explanations consistent with these observations that translation produces a positive factor required for transcription[22]. Thus, the results so far from these *in vitro*

systems are consistent with the notion that a product of the histidine operon is involved in regulating its own synthesis. In one case, however, this product is thought to be the first enzyme and a negative element in control, whereas in the other, this product is an unspecified positive factor. A combination of the two is also a possibility.

Similar developments have occurred in the study of the isoleucine–valine (*ilv*) biosynthetic system. This system involves multivalent repression[23,24] in a branched set of pathways[25] and is, therefore, more complex than the histidine system. As is the case for the histidine operon, no classical aporepressor has been identified for the isoleucine–valine system. On the basis of biochemical data Hatfield and Burns[26] suggested a model of repression control for the *ilvADE* operon in *S. typhimurium* that involves the first enzyme of the isoleucine pathway (threonine deaminase, EC 4.2.1.16), leucyl-tRNA, valine, threonine and isoleucine. According to this model, which now has been modified and extended to cover regulation of the other *ilv* operons in *E. coli* and *S. typhimurium*[27], the first enzyme is an aporepressor and the multivalent corepressors are isoleucyl-tRNA, leucyl-tRNA and valyl-tRNA. On the other hand, Levinthal *et al.*[28] have described a regulatory mutant of *E. coli* in which the expression of the *ilvADE* operon is diminished and unresponsive to variations in the branched chain amino acids. This phenotype results from a single point mutation in the structural gene for the first enzyme of the isoleucine pathway. Based on these and other genetic results, Levinthal *et al.*[28] suggested that the first enzyme is a positive element controlling expression of the isoleucine–valine system.

A defective transducing phage harbouring the *ilv* genes[29] is being used for *in vitro* transcription and coupled transcription–translation assays, to study the molecular events in the regulation of the isoleucine–valine biosynthetic system of *E. coli*.

As this brief introduction indicates, there are repressible biosynthetic operons whose regulation involves a classical, constitutively synthesised aporepressor. There also are examples of such systems that involve autogenous regulation, whereby a regulatory protein directly modulates expression of its own structural gene[30]. Although in no case has it been demonstrated that either of these is the sole mechanism of control, the question arises: what are the functional implications of these two established modes of regulation? This question cannot be answered by comparing directly two representative systems (for example, tryptophan and histidine) because there may be still other elements involved in their control and because the systems are different in many ways that are irrelevant to a comparison of the two modes of regulation *per se*. An answer requires a more controlled comparison in which the two systems are identical in every respect except for the difference in a regulatory mechanism. This is difficult to do experimentally. At present a more practical approach is to compare mathematically models that accurately represent the different types of regulation. Such comparisons have been made and the details, unnecessary here, are available[31]. Before presenting the results it will be useful to enumerate the criteria for functional effectiveness that have been used in comparing the various models.

Criteria for functional effectiveness

Just as numerous chemical and physical criteria make possible characterisation of the molecular components of biological systems, well defined criteria make possible characterisation of the functional behaviour of an integrated system. For simplicity, in the analysis that follows I deal specifically with the regulation of unbranched pathways for the biosynthesis of amino acids. The following criteria for functional effectiveness can be formulated for these systems. It should be noted that none of these criteria

assumes anything about the type of regulatory mechanism involved.

(1) Minimisation of the change in the level of end product as it shifts from one steady state to another in response to a change in demand for end product. This implies that the end product will not be depleted to such an extent that its rate of utilisation is limited when the demand is increased.

(2) Responsiveness to change in the availability of initial substrate. This is essential for the redistribution of common intermediary metabolites that occurs in response to a changing environment when the available carbon is limited.

(3) Reduction of enzyme synthesis when the end product is supplied exogenously. Since the biosynthetic enzymes become superfluous when the end product is available preformed in the environment, the importance of this criterion for cellular economy is obvious.

(4) Stability. Presumably one of the prime functions of pathways synthesising amino acids is to provide a relatively constant supply of their end products for protein synthesis. An effective system would not oscillate wildly, starving the organism for end product during one phase and overproducing and wasting it in the next. The impaired growth of mutants exhibiting such instability is readily apparent[32].

(5) Temporal responsiveness to change. The regulatory mechanism should enable the system to respond quickly to changes in its environment.

(6) Insensitivity to perturbations in the structure of the system itself. Small changes in the system may be the result of mutations in structural or regulatory genes, errors in transcription or translation of the genetic information, or physical influences such as temperature shifts. These changes tend to exert a deleterious effect on the cell and, as Sonneborn suggested[33], cells "buffered" against such harmful effects are likely to have a selective advantage.

Repressor-controlled systems

Models of classical and autogenous regulation are represented schematically in Fig. 1. In the classical Jacob-Monod model the structural gene for the regulatory protein is located in a separate transcriptional unit and is itself unregulated, whereas in the model of autogenous regulation one of the protein products of the operon is the regulator, which therefore directly controls expression of its own structural gene. For purposes of comparison these models are assumed to be equivalent except for their differences in regulatory interaction.

These two models can be compared for a wide variety of conditions, and because there are several criteria to consider, a meaningful tabulation of all the results presents a problem. Figure 2, however, is a rather simple diagram that conveniently summarises many of these results. In this plot the vertical axis represents the strength of the contribution of end product to the regulation while the horizontal axis represents the strength of the autogenous contribution. Each point in this two-dimensional space represents a different system with distinctive properties. Nevertheless, this space can be divided into subclasses of systems that have similar properties.

In repressible systems that utilise a repressor mechanism, the end product has a negative effect on transcription, and the autogenous contribution is also negative. Since both contributions are negative, only the lower left hand quadrant of Fig. 2 needs to be considered. The vertical axis in this quadrant is the locus of points representing systems with constitutively synthesised repressor, since the autogenous contribution is zero. Line *b* represents another important classification. The position of this line is determined by analysing the local stability of these models. All systems represented by points above line *b* are stable (if perturbed momentarily, they will return to their predisturbance condition), whereas all systems represented