Four main results emerged from this work. These may be seen from Fig. 2. In the first place, there were no significant differences between the groups in amount of exploration during the 20-min. trial of day 1. Nor were any differences found between the reactive and non-reactive rats on day 1. (The results were analysed by non-parametric techniques.)

Secondly, a comparison of the mean amount of exploration on day 1 with that on day 2 revealed a significant increase for the 15 rats taken as a whole. Further analysis showed that the reactive rats were mainly responsible for this, in that their day 1 to day 2 increase was significant ($P = 0.05$), whereas that of the non-reactive animals was not.

Thirdly, differences between the groups failed to reach significance on day 3. However, on day 4, the difference in exploration between groups $A(20)$ and $C(60)$ during the *first* 20 min. was highly significant ($P = 0.004$). The difference between groups $A(20)$ and $B(40)$ did not reach an acceptable level.

Lastly, the differences in mean exploration scores after a period of 9 days absence from the maze reveal a decrement for those rats given extended periods of exploration during the first phase of the experiment. The difference between $A(20)$ and $B(40)$ was significant at $P = 0.05$ (two-tailed test) ; the difference between group $A(20)$ and group $C(60)$ was significant at a more acceptable level ($P = 0.01$). However, the mean difference between group $B(40)$ and group $C(60)$ was not significant.

The first result, namely, the day 1 to day 2 increase in exploration, has not been reported, previously, by other investigators. However, it has been suggested that novel stimuli may elicit fear as well as curiosity[6], and this effect may be due, therefore, to the extinction of fear responses elicited during the first trial. This view gains support in that emotionally 'reactive' rats manifest this increase more markedly than 'non-reactive' animals. Further research is needed to test this hypothesis.

With regard to a controversy concerning the permanency of a decline in exploratory tendencies after repeated exposure, the results of this experiment lend support to Berlyne's position. They suggest that Montgomery failed to allow rats sufficient time to explore a novel environment to the point at which a more permanent decrement occurs. More research is needed to confirm the adequacy, as opposed to the usefulness, of Berlyne's hypothesis. However, a neurophysiological basis for the inhibitory concepts of this theory may be found in experiments[7] concerning habituation of the arousal response in cats.

I am indebted to Dr. Peter McKellar for supervision and help in conducting a series of experiments of which the present experiment is a part.

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THE AFFINITIES OF THE NEW OLDUVAI AUSTRALOPITHECINE

DR. L. S. B. LEAKEY recently reported in *Nature*[1] the discovery of an essentially complete hominid skull without mandible from site *FLK* at Olduvai Gorge. He regards the specimen as an australopithecine that differs more from either of the two known genera, *Australopithecus* and *Paranthropus*, than these two differ from each other. He therefore erected the genus *Zinjanthropus* to accommodate the new specimen.

The description consists largely of a list of twenty 'major' differences between the new specimen and the two previously known genera. Some of these points cannot be dealt with as they are briefly stated in terms which are not useful by themselves for comparison. Others, for example, continuous nuchal crest, enlargement of the mastoid area, prominent temporal lines, large areas for masseter attachment, etc., do not each represent a separate difference ; all are reflexions of the fact that this specimen is a little larger and more muscular than the known South African specimens of *Paranthropus*. In at least one case (nuchal crest) comparison with the latter specimens is not possible since there is no known male specimen with the relevant area preserved. The remainder are not real differences and will be dealt with briefly :

(1) The inion is lower relative to the Frankfort plane : In both *Australopithecus* and *Paranthropus* the base of the external occipital protuberance is almost exactly in the Frankfort plane, as seems to be the case with the Olduvai specimen.

(2) The posterior wall of the occipital bone rises more steeply to form, with the parietals, a very high-vaulted posterior region of the skull : This is also the case in *Paranthropus*, less so in *Australopithecus*. *Paranthropus* has an almost spheroidal brain-case which is relatively low and narrow anteriorly but steep-sided and higher posteriorly. *Australopithecus* has a brain-case more nearly like that of a dolichocephalic modern hominine. The Olduvai specimen has the *Paranthropus* type of brain-case.

(3) The form of the tympanic plate is different : Dr. Leakey demonstrated this point to me on the specimen to make clear his meaning. This feature is variable in *Paranthropus* and includes an instance of close resemblance to the Olduvai specimen. The observed range of variation is illustrated in Fig. 1. Being thus variable, it is in any event a feature of low phyletic valence.

(4) The very unusual position of the nasion— almost coinciding with glabella : This is true of *Paranthropus* and in at least some cases of *Australopithecus* also. In *Paranthropus*, as in the Olduvai specimen, the nasals are relatively very wide near the nasion.

(5) The very great absolute and also relative width of the inter-orbital area. The proportionate width of the inter-orbital area to that between the external orbital angles is 26.6 in the Olduvai specimen ; 26.2 (*SK* 846), 25.3 (*SK* 48) in two specimens of *Paranthropus*. A single specimen of *Australopithecus* gave a value of 24.1, while a random sample of eight
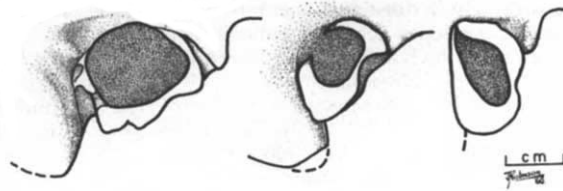
Fig. 1. Variation of the tympanic bone at the lateral end of the external auditory meatus in *Paranthropus* from Swartkrans (*SK* 48, *SK* 52 and *SK* 848). The Olduvai specimen resembles in this feature the condition illustrated in the middle diagram

modern human skulls gave a range of 23·4–30·5. No taxonomic significance can therefore be attached to this point on the present evidence.

(6) The very deep palate which is even more markedly like that of *Homo* than *Australopithecus*, and is quite unlike the form seen in *Paranthropus* : In *Homo*, the degree of vaulting of the hard palate is variable, but the difference in depth at the incisive fossa and the back of the palate is normally relatively slight. This is true also of *Australopithecus*. The palate of *Paranthropus* differs in that it slopes more markedly ; that is, there is always an appreciable difference between the anterior and posterior depths —in some cases there is no depth at all anteriorly, in others the anterior depth is appreciable. The Olduvai specimen shares this characteristic of relatively much greater posterior compared to anterior depth, reflecting the *Paranthropus* condition, not that of *Homo* and *Australopithecus*.

(7) The shape and arrangement of the zygomatic process of the maxilla : The Olduvai specimen has a relatively poorly developed zygomatic process, the lower border of which passes almost horizontally from the zygo-maxillary suture to the main body of the maxilla. In some specimens of *Paranthropus* the process passes from the zygo-maxillary suture downward and medial-ward at a fairly sharp angle like an inverted flying buttress. However, *SK* 52, of the same dental age as the Olduvai specimen, has a trace only of the buttress and *SK* 846 (mature adult) has no trace of it, as in the Olduvai specimen.

(8) The relatively greater reduction of the canines in comparison with the molar-premolar series than is seen even in *Paranthropus* : As the marked change of proportion between anterior and cheek teeth occurs in *Paranthropus* and the Olduvai specimen between canine and P^3, the degree of reduction can be measured by the ratio between the modules of these two teeth. The ratio for the Olduvai specimen is 64·9 while that for three specimens of *Paranthropus* ranges from 61·8 to 78·8.

(9) In the species diagnosis Leakey refers to the presence of a sagittal crest "at least posteriorly". The reason for this statement is not clear, since the crest occupies a position identical to that in *Paranthropus*—on roughly the middle third of the distance between glabella and inion. In neither form is the sagittal crest known to reach as far back as the planum occipitale or even the posterior part of the sagittal suture.

It seems to me that the most fruitful approach to an understanding of the australopithecine skull, within the framework of hominid structure, is in terms of diet and the nature of the dentition. *Australopithecus*, as an omnivore eating at least a moderate amount of flesh, has a dental apparatus very similar to that of the older hominines. The relative sizes of the teeth along the tooth row are closely similar, as is the arrangement of the dental arcades. The

anterior teeth, especially the canines, are well developed, but the post-canine ones only moderately so. The skulls are also similarly constructed except for the relatively small cranium, compared to the face, of *Australopithecus*.

In *Paranthropus* the situation is very different. Here the anterior teeth, set in an almost straight line across the front of the palate, are appreciably reduced in size compared to those of *Australopithecus*, while the post-canine teeth are appreciably larger. This difference in arrangement and proportion is very striking and is characterized by the very small canine tooth set firmly against a massive premolar. All this must clearly have functional meaning. The massive crushing and grinding teeth, the relatively unimportant anterior teeth and frequent damage to the enamel which could only have been caused by small, very hard particles (presumably grit), and the large size of the animal suggest a predominantly vegetarian diet. Concentration of heavy dental function in the post-canine region has strongly modified the skull architecture. The massive cheek teeth, especially the molars, have strongly developed root systems and hence are set in heavy bone, and the back of the palate is relatively deep. Owing to the heavy chewing forces, the palate is thick, the jaws are massive, especially where supporting the cheek teeth, the zygomatic arches are strongly built, the circum-orbital bone is strong in the stressed areas, the strongly stressed pillars on either side of the pyriform aperture are thick and the medial and lateral pterygoid plates, especially the latter, are large and strong. However, the large dental battery requires heavy musculature to operate it—hence further changes from the *Australopithecus* and hominine pattern. The areas of origin and insertion of these muscles are sturdy ; hence the large surface area of the mandibular ramus, the massive zygomatic arch—which also is widely spaced from the brain-case to allow for the very large temporal muscle—large medial and lateral pterygoid plates, clearly defined temporal lines, sagittal crest and apparent prominence of the supraorbital tori. The large muscles associated with the large and chunky animal result in well-defined muscular ridges on the occiput and the prominence of the mastoid area—assisted by the large temporal muscles which necessitate appreciable lateral extension of the zygomatic arch. It is probable also that the large temporal muscles have influenced the shape of the brain-case anteriorly to help produce the low and narrow shape characteristic of *Paranthropus*. As is usual in relatively massive skulls where large surface area is necessary, some reduction of weight has occurred by increased pneumatism. The mastoid region (not the mastoid process alone) is strongly cellular and the air spaces in the skull base, the maxillæ and the frontal bone are all very large.

The curious and characteristic features of the *Paranthropus* skull, which parallel some of those of the gorilla skull and mark it off so clearly from that of *Australopithecus*, are all functionally related and determined largely by the specialized diet of this creature as compared to all other known hominids. These functional and structural differences indicate clear adaptational differences between the two forms and hence also differences of evolutionary direction. In modern systematics, adaptational differences of this order and nature are normally accorded generic rank.

The features of the Olduvai specimen fit the *Paranthropus* pattern as here outlined very accurately—

the differences being almost entirely of the sort shown to be variable within a single population by the sample of nearly 200 specimens of *Paranthropus* now in the collections of the Transvaal Museum. The chief feature of the Olduvai form which does not fall within the observed range of variation of this collection is size. The best size comparison is with the only male specimen with good teeth which has P^3–M^1 preserved in sequence and is of the same dental age as the Olduvai specimen. The latter is only 8·4 per cent larger. The average percentage difference for five skull and dental series dimensions compared to those of a fully adult female skull is 17·4 per cent. As Schultz has shown in a number of papers, intra-specific variation in measurable primate anatomical characters can often greatly exceed the above values.

The validity of separate specific status is not clear on the basis of the single specimen, and it is perhaps wisest to leave it as distinct. In the light of the above analysis, however, separate generic status seems unwarranted and biologically unmeaningful. I therefore propose that the name of the Olduvai form be *Paranthropus boisei* (Leakey).

<div align="right">J. T. ROBINSON</div>

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    Pretoria.

¹ *Nature*, **184**, 491 (1959).

THE exact taxonomic label that should be applied to the skull that I have named *Zinjanthropus*, from Olduvai, and which I described in *Nature* of August 15, 1959, seems to me relatively unimportant at the moment. Inevitably, different scientific workers have different ideas of what characters justify specific, generic, and even superfamilial rank. After all, this is purely a question of artificial labels.

Dr. Robinson and I agree that *Zinjanthropus boisei* is closely related to the Australopithecinae ; we agree that it has certain resemblances to *Paranthropus*, and we disagree mainly in that he believes the differences to be insufficient to justify separate generic rank, while I think they do.

It is hard enough to reach agreement among zoologists on the taxonomic status of living primates, under conditions in which we possess the skull, skeleton, skin and viscera for study, and it will always be much more difficult to do so when we have only fossils to guide us. I can only say that the very considerable additional work that I have done on the *Zinjanthropus* skull since my preliminary report in *Nature* has greatly strengthened my view that it is entirely different from *Australopithecus* and *Paranthropus*, differing from both these genera more than they do from each other.

I do not feel that any useful purpose would be served by entering into a long discussion with Dr. Robinson in *Nature* at present, since the more detailed study of the Olduvai skull which is now in hand will not, I hope, be too long delayed. However, Dr. Robinson makes certain statements which may mislead those who read them, unless I comment on them. I will therefore do so as briefly as possible.

First of all, whereas in *Paranthropus* and *Australopithecus* (as Dr. Robinson says) the external occipital protuberance lies more or less on the Frankfort plane, in *Zinjanthropus* it lies below it.

Robinson's description of the brain case of *Paranthropus* as "almost spheroidal", but also "relatively low and narrow anteriorly but steep-sided and higher posteriorly", does not seem to make sense, for the two statements seem to cancel each other out. In any event, such a combined description does not fit the brain case of *Zinjanthropus*.

Robinson illustrates the range of the tympanic plate (see in profile), in *Paranthropus*. None of these three illustrations closely resembles the tympanic plate of *Zinjanthropus*, although the one to the left appears to be rather closer than the middle one.

Without knowing the points at which Robinson measures inter-orbital width and external orbital width, I cannot comment upon his comparisons of his *Paranthropus* figures with mine for *Zinjanthropus*.

As to the morphology of the palate, I do not know upon what evidence Robinson is basing his statement, since I have published no measurements of the palatal depth in *Zinjanthropus*. I must repeat, however, quite categorically, that the morphology of the *Zinjanthropus* palate in no way resembles that of *Paranthropus*.

I cannot accept Robinson's statement that the zygomatic process of the maxilla in *Zinjanthropus* is "relatively poorly developed" ; I would say rather, as I have said before, that it is developed in an entirely different morphological manner from *Paranthropus*.

As regards the position of the sagittal crest, in *Zinjanthropus* it ceases to be a crest and divides into two temporal lines well behind the line drawn vertically through the ear when the skull is on the Frankfort plane. In *Paranthropus* (in all the published photographs), the sagittal crest extends a long way forward of such a vertical line through the ear when the skull is on the Frankfort plane, and it is therefore wrong to say, as Robinson does, that "the crest occupies a position identical to that in *Paranthropus*".

Finally, I do not understand the significance of a comparison of "the ratio between the modules of these two teeth", that is, the canine and P^3. Robinson has defined a module as the sum of the length and breadth of a tooth divided by two, and I am at a complete loss to understand how the ratios of modules can have any significance. It must be obvious that one can have on one hand a canine tooth 16 mm. long and 6 mm. wide (module equals 11), and a premolar 9 mm. long and 7 mm. wide (module equals 8), while in another specimen one could have a canine which measured 11 mm. × 11 mm., and a premolar which was only 5 mm. long and 11 mm. wide, yet the ratio of the modules in the two sets of teeth would be identical, but completely without significance.

In any event, the ratio between the canine and the premolar alone cannot have any bearing upon the relation of the canine size to the total molar–premolar series, unless the premolar bears a constant relation to the total post canine series.

I therefore repeat my statement that in *Zinjanthropus* there is a relatively greater reduction of the canines in comparison with the total molar–premolar series than is seen in *Paranthropus*, and maintain that Robinson has in no way disproved this statement.

I agree with Robinson that we need to study the *Australopithecus* skull structure and dentition in terms of diet and mode of life, and I shall certainly do so as far as *Zinjanthropus* is concerned in my fuller report.

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