A FOSSIL ANT COLONY: NEW EVIDENCE OF SOCIAL ANTIQUITY*

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The fossil remains which will be described below are of exceptional interest for two reasons: (1) they are the first ant fossils to be reported from Africa south of the Sahara and (2) they comprise what appears to be a fragment of a colony preserved as a unit, thus constituting the first fossil insect colony ever recorded. From the sample we have been able to make measurements of the worker polymorphism and certain deductions concerning the biology and social structure of an ant species as it lived in the lower Miocene over 30 million years ago.

We are indebted to the Trustees and Director of the Coryndon Museum for the opportunity to study this unique material, which was collected by Dr. and Mrs. L. S. B. Leakey in the Lower Miocene deposits of Mfwangano Island, Lake Victoria, Kenya. Professor A. E. Emerson first identified the specimens as ants, realized their potential significance, and forwarded them to us for examination. The research program of which the study became a part is currently supported by Grant No. GB 1634 from the National Science Foundation.

Oecophylla leakeyi Wilson and Taylor, new species
(Subfam. Formicinae, Tribe Oecophyllini)

Diagnosis. Distinguished from all other known species of the genus, living and fossil, by the large size of both worker subcastes; by the massive, cordate head of the major worker; and by the presence of well developed ocelli in the major worker. All of these characters are illustrated in Figure 2.

The mesosoma is stouter than in the two living species *(longinoda, smaragdina)* and in the Miocene species *sicula;* in this regard its structure is closer to the Eocene species *brischkei.* The petiole is not well enough preserved in any of the *leakeyi* specimens to permit a meaningful comparison with the same structure in other species. The gaster has the form typical of all other known members of the genus.

The *holotype* is the major worker head illustrated in Figure 2 and Plate 11. Its maximum width taken perpendicular to the long axis is

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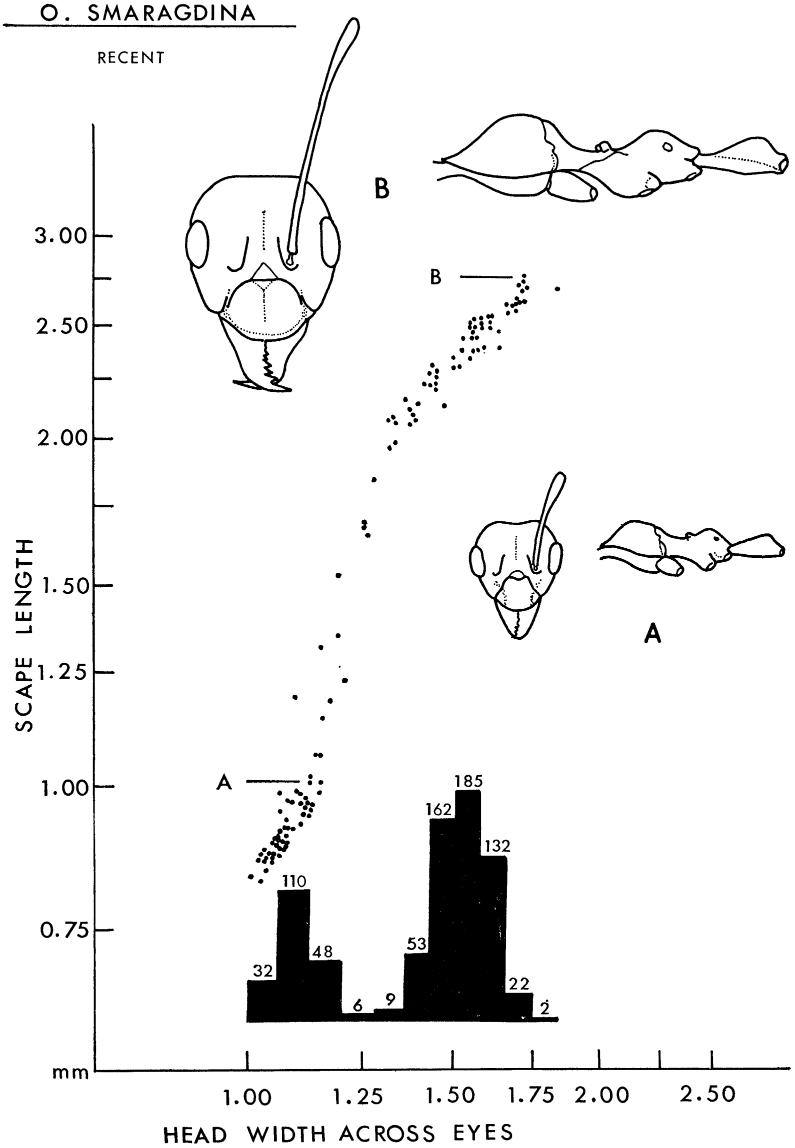


Figure 1. *O. smaragdina.* (For explanation see opposite page).

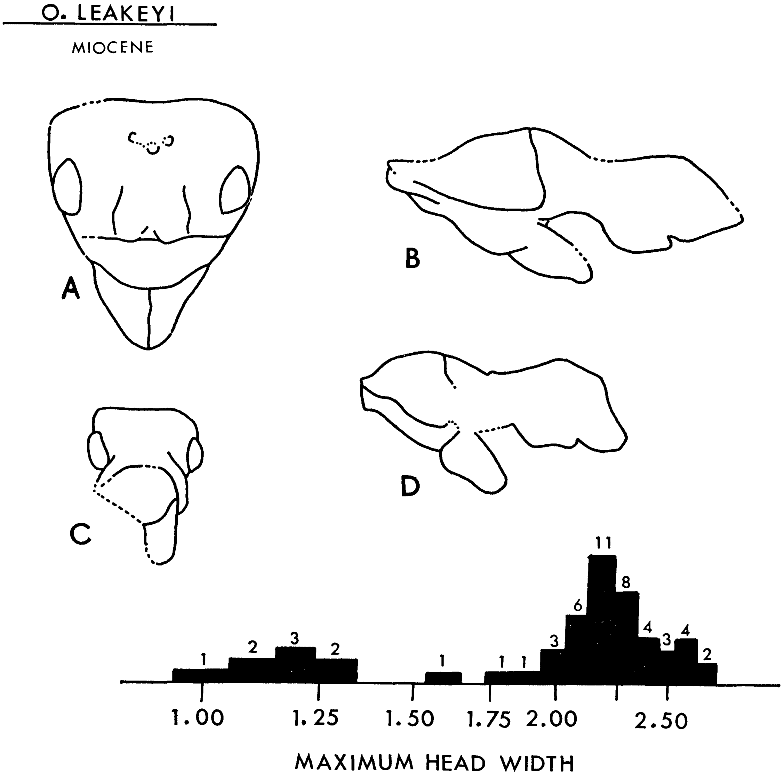


Figure 2. *O. leakeyi*

Figures 1-2. *The comparison of worker polymorphism in the Miocene Oecophylla leakeyi with that in the living O. smaragdina.* In Figure 1 (opposite page), the size frequency curve of a large random sample from a single colony of *O. smaragdina* from Assam is given in head width units plotted logarithmically. The mesosomas and petioles of selected minor and major workers are also shown, as well as the double logarithmic plot of the scape length against head width. (Modified from Wilson, 1953). In figure 2 (above) similar data from the fossil *leakeyi* colony are given in scale with Figure 1. Pupal worker head widths are used but are closely comparable to adult worker head widths. Scape length could not be measured in this material. A, head of holotype major worker (imaginal), B, mesosoma and petiole of a major worker (imaginal), C, head of a minor worker (pupal), D, mesosoma and petiole of a minor worker (imaginal).

2.36 mm.; its length, taken from the posteriormost level of the occiput to the anteriormost level of the clypeus, is 2.19 mm. This specimen agrees well in size and structure with the heads of entire worker pupae. There can be no doubt that it is from a worker specimen.

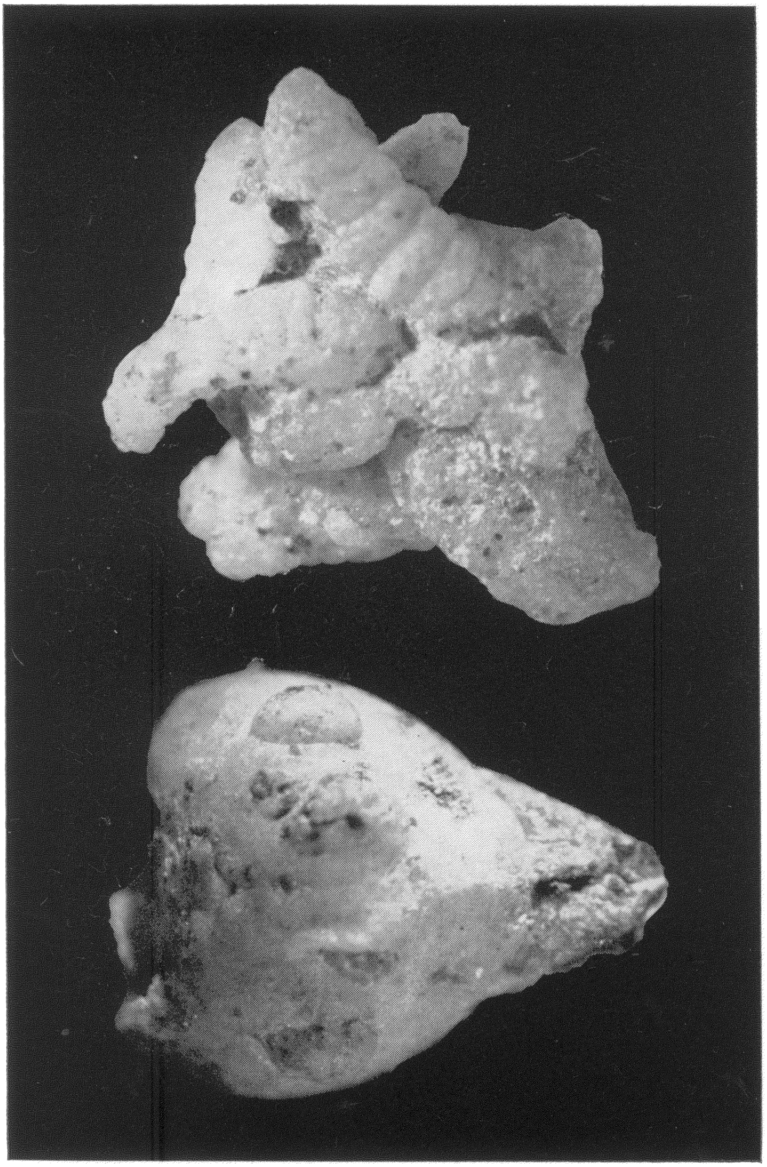
Material examined. A total of 438 specimens, including 197 larvae (perhaps including some prepupae), 105 worker pupae, 24 worker heads, 48 worker mesosomas, and 64 worker gasters. Even if the various worker body parts are assumed to have resulted from dismemberment of a smaller number of workers, the total number of individuals represented in the collection is at least 197 + 105 + 64 = 366. All of these pieces were collected together by Dr. and Mrs. Leakey in a volume of matrix about 2 feet square and several inches thick, in a Lower Miocene Deposit on Mfwangano Island, near Rusinga Island, in the Kavirondo Gulf neighborhood of Lake Victoria, Kenya. The geology of this and similar deposits in the area has been briefly reviewed by Chesters (1957). The holotype and some paratypes will be deposited in the British Museum (Natural History). Other paratypes will be placed in the ant collection of the Museum of Comparative Zoology, Harvard University, and in the Centre for Prehistory and Paleontology, Coryndon Museum, Nairobi, Kenya.

The Zoogeography of *Oecophylla*

The genus is represented by two living species: *O. smaragdina* (Fabricius) which ranges from India to the Solomon Islands and Queensland; and *O. longinoda* (Latreille), which occurs throughout most of tropical Africa. These are the famous "weaver ants" whose workers employ the mature larvae as shuttles to bind the nests together. The nests are always arboreal and consist of clusters of green leaves folded over and fastened together with larval silk. A single mature colony usually occupies many such nests scattered through one or more trees. The colonies are highly territorial, defending their trees against other ant species and larger invading animals. The workers are exclusively arboreal in their foraging, collecting varied insect prey and attending coccids. The two species are very similar in both morphology and behavior, but sufficient minor differences in morphology exist to justify their specific separation. Over most of their ranges both species are very abundant and highly adaptable. They occur in rain forests, groves of crop trees, and even shade trees along urban streets. The most complete and general studies of the biology of the genus are contained in the works by Ledoux (1950, 1954) on *O. longinoda*. Bhattacharya (1943) and Brown (1959) have reported on special aspects of the ecology and physiology of *O. smaragdina.* Variation and taxonomic relationships of the two species are discussed in the reviews of Emery (1921) and Wheeler (1922).

Oecophylla is well represented in Tertiary fossil deposits. *O. brishkei* Mayr, which closely resembles the modern forms, is moderately abundant in the Baltic amber, of Eocene age. It was represented by 50, or 0.4% of all of the 11,678 Baltic amber ants examined by G. Mayr and W. M. Wheeler jointly (Wheeler, 1914). A second, more divergent species, *O. brevinodis* Wheeler, was represented in the collections by a single specimen. Another species, *O. sicula* Emery, has been described from Upper Miocene deposits in Sicily. The species thus far mentioned form a morphocline in the increase of length of the legs, antennae and petiole, and the narrowing of the metathoracic constriction. This morphocline, which follows the geologic sequence, runs as follows: *brevinodis* → *brischkei* → *sicula* → *longinoda* (together with *smaragdina*). It seems reasonable to conclude that the species exhibit the approximate phylogenetic succession that must have occurred in the evolution of the modern species of the genus. *O. leakeyi* is a somewhat divergent member with reference to this succession, in its larger size and retention of ocelli in the major worker caste. It would appear to fall nearest to *brischkei* in the degree of mesosomal and appendage elongation. Two other species have been named on the basis of queens found in the Miocene shales of Europe: *O. obesa radobojana* (Heer) from Radoboj, Croatia; and *O. praechara* (Foerster) from Brunstatt, Alsatia. The precise relationships of these forms cannot be determined, although Mayr (cited by Wheeler, 1914) stated that *radobojana* cannot be distinguished from *smaragdina.* No New World fossils of *Oecophylla* are known, and the genus is notably absent from the rich Miocene collections from Florissant, Colorado, described by Carpenter (1930).

In sum, the picture that emerges of *Oecophylla* is that of a morphologically stable Old World genus that has persisted through most of the Tertiary with very little speciation. *Oecophylla* is related to at least two other relict, arboricolous Old World genera that date to the Eocene: *Dimorphomyrmex* and *Gesomyrmex.* Furthermore, it is not far distant from *Gigantiops,* a remarkable terricolous genus now limited to the South American rain forests. It seems appropriate to regard *Oecophylla* as both specialized and caught in an evolutionary cul-de-sac. We can speculate that its unique specializations have permitted it to remain abundant and widespread — but at the expense of blocking further significant evolution and speciation.



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The Polymorphism and Inferred Biology of *Oecophylla leakeyi*

There are good reasons to regard the Mfwangano Island material as a sample from a single colony, perhaps the contents of one nest preserved intact. In evidence is the fact that such a large number of specimens in all stages of development were recovered from a volume of roughly only one cubic foot of rock. Also, and equally important, many of the immature forms are beautifully preserved in clusters. A single group of newly hatched larvae are joined together in a typical "microlarval pile" (Plate 10). These groupings could have been preserved only if the colony had been subjected to a minimum of disturbance prior to fossilization.

When we measured the head widths of all of the adequately preserved pupal workers (the measurable adult workers were too few for our purposes) the results were startling. As shown in Figures 1 and 2 the size-frequency distribution is of essentially the same form as in the living species *O. smaragdina.* This particular distribution includes the following two important features: the separate distributions of the minor and major worker castes are nearly but not completely nonoverlapping, and the majors are *more numerous* than the minors. So far as is known, the *Oecophylla* type of distribution is peculiar to the genus among living ants (Wilson, 1953). The polymorphism in *O. longinoda* was shown independently by Weber (1949) and Ledoux (1950) to be correlated with a division of labor in which the majors do most of the foraging and nest defense and the minors serve more as nurses. The allometry of the living *Oecophylla,* involving a narrowing of the metathoracic constriction with increase in size (instead of the reverse), is also unusual if not unique among living ant species. The same kind of allometry is exhibited by *O. leakeyi.* Thus *O. leakeyi* possessed the same unusual and quite specialized features of worker polymorphism retained by the modern members of the genus. This first direct demonstration of the nature of polymorphism in an extinct ant species shows *Oecophylla* to be conservative not only in morphology but in basic social organization.

But this is not the end of the story. Further findings indicate that the *leakeyi* nest was arboreal, just as in modern species. Numerous larvae, pupae, and adults are attached directly to well preserved leaf frag-

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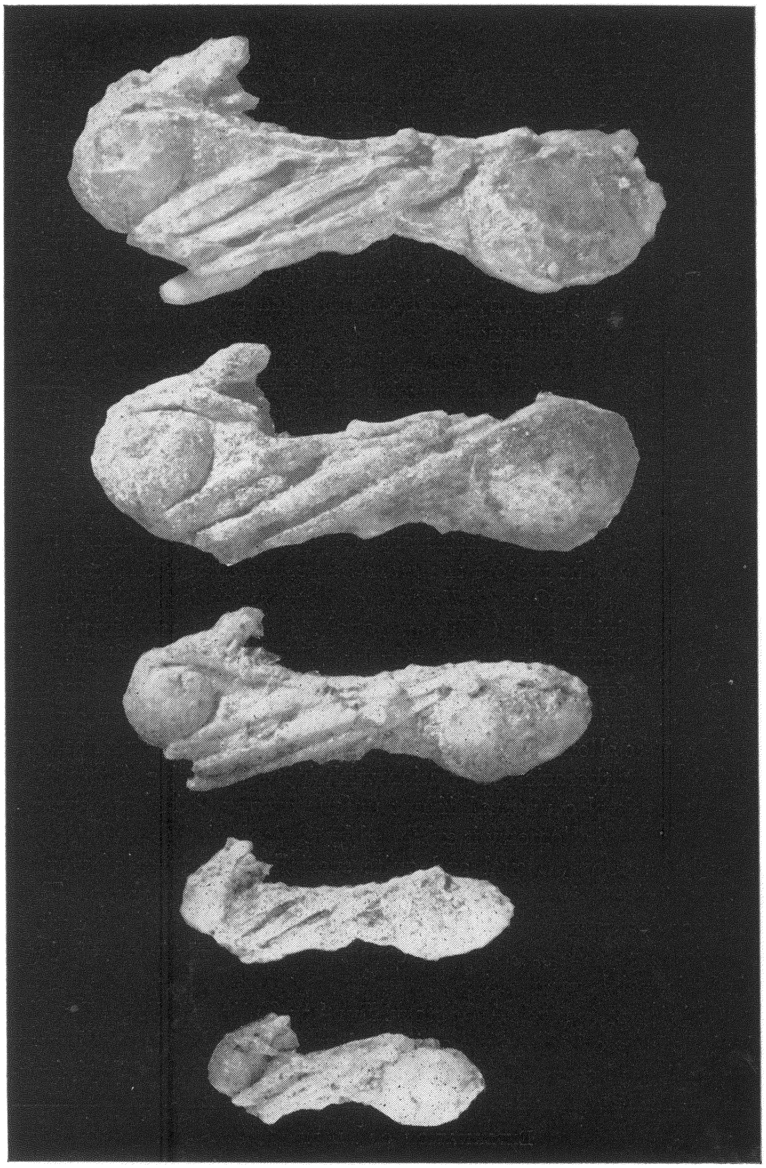
Explanation of Plate 11

Left: head of holotype major worker, *O. leakeyi. Right:* fossilized microlarval pile of *O. leakeyi.* The maximum diameter of the larval pile is approximately 3.4 mm.



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ments. Also, the *leakeyi* pupae are not enclosed in cocoons, a negative character shared with the modern species of the genus. The absence of cocoons is a rare and probably derived character within the subfamily Formicinae (Wheeler, 1915). Cocoons are omitted by many of the diverse species of *Polyrhachis* that are arboreal and use silk produced by their larvae for nest construction. They are also omitted by certain twig-dwelling species belonging to such genera as *Camponotus (Colobopsis)* and *Gesomyrmex;* the latter genus is included on the basis of a single naked pupa recorded by Wheeler (1929). Cocoons are also lacking in two related terricolous genera, *Prenolepis* and *Paratrechina.* The great majority of formicine genera, however, are both terricolous and cocoon-makers. The absence of cocoons is, therefore, correlated, but not perfectly, with the arboricolous habit. Additional evidence favoring the proposition that the *leakeyi* colony was arboricolous is the very fact that the colony was preserved intact. It is very difficult to imagine how a subterranean or log-nesting colony could have been preserved as a unit; but it is much easier to imagine how an arboreal nest, especially the kind constructed by modern *Oecophylla,* could have broken off, dropped into the water, and been preserved with little further disturbance. The small ratio of workers to immatures suggests that the former were able to escape in part while the latter remained trapped inside the drowned nest.

Although the foregoing considerations are admittedly tenuous, something more definitive can be said about the habitat in which the *leakeyi* colony lived. The species was part of a rich arthropod fauna. The Leakeys *(in litt.)* found it in association with many hundreds of other soft-bodied insects of diverse orders, as well as arachnids. Very little of this interesting fauna has been studied. There is also abundant associated plant material. In a preliminary study of the Mfwangano and Rusinga Islands plant fossils, Chesters (1957) discerned a minimum of 17 families and 21 genera of which five are fern genera. The majority of the fossils represent living African tropical genera. "Much of the material awaiting detailed examination will probably prove to be unidentifiable owing to its mode of preservation as crystalline casts. But the report here published does give a representative picture of a Miocene flora closely akin to that of tropical Africa at the present day. . . . The large number of lianas suggests a gallery-type forest in which trees festooned with climbers overhung the water-course."

EXPLANATION OF PLATE 12

Fossil pupae of *O. leakeyi* of various sizes. The actual total length of the smallest specimen is about 4.0 mm.

SUMMARY

Oecophylla leakeyi Wilson and Taylor is described as a new species. It is from the Lower Miocene deposits of Mfwangano Island, Kenya, and is the first species of fossil ant described from Africa south of the Sahara. The type series, which contains worker subcastes, pupae, and larvae in all stages of development, is interpreted as comprising a colony fragment, the first ever recorded as a unit in the social insects. From statistical and morphological studies of the three-dimensional specimens it is concluded that the worker polymorphism conforms to the essential features that uniquely characterize the living *Oecophylla* species within the modern ant fauna. This constitutes direct evidence of the stability of a specific social system through a considerable period of time, i.e. 30 million years or longer. Other evidence is cited which suggests that the *leakeyi* colony also resembled the modern species of *Oecophylla* in that it nested arboreally in tropical rain forest.

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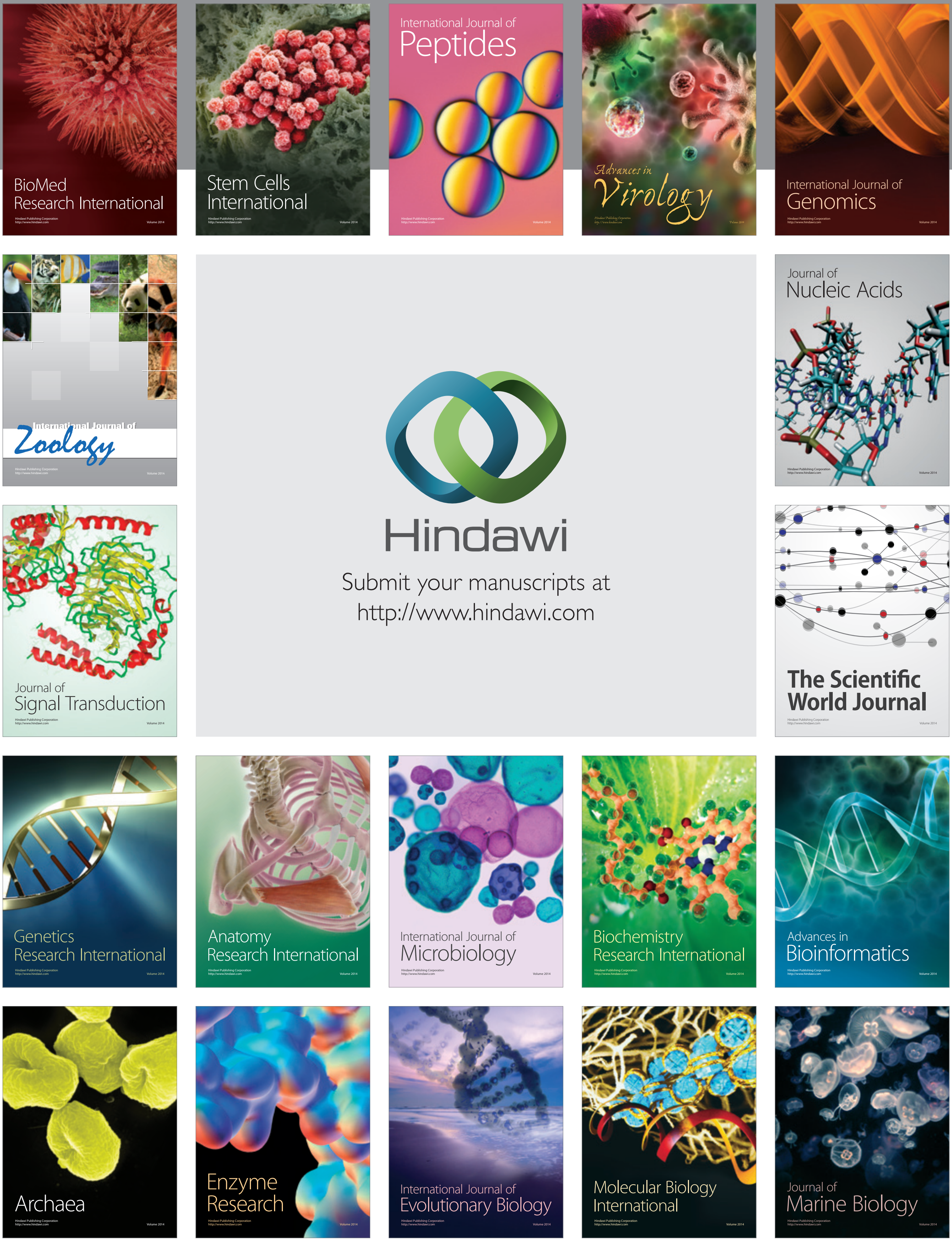

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