CHROSIOTHES TONALA (ARANEAE, THERIDIIDAE): A WEB-BUILDING SPIDER SPECIALIZING ON TERMITES*

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INTRODUCTION

A variety of spiders in web-building families or descended from web-building ancestors are specialist predators on certain types of prey. Some are spider specialists, such as the theridiids *Argyrodes* (Clyne 1979, Eberhard 1979, Shinkai and Shinkai 1981, Whitehouse 1987), metids (Bristowe 1958, Jackson and Whitehouse 1986), and the araneid *Chorizopes* (Eberhard 1983). Others are ant specialists, such as deinopids (Robinson and Robinson 1971, Coddington and Sobrevilla 1987) and the theridiid *Euryopis* (Carico 1978), and perhaps also the theridiids *Steatoda* (Hölldobler 1970), *Dipoena* (Jones 1983, Shinkai 1984), and *Saccodomus* (McKeown 1953). Species in several araneinine genera are apparently moth specialists (McKeown 1953, Robinson and Robinson 1975, Eberhard 1980, Stowe 1986).

This note documents an additional case of prey specialization by a web-builder that involves an especially unlikely combination of spider and prey: a tiny species in the family Theridiidae, *Chrosiothes tonala* Levi, and the wingless worker and soldier castes of the termite *Tenuirostritermes briciae* (Snyder) which builds underground nests (Nutting 1970).

MATERIALS AND METHODS

Observations were made during the wet season at the Estación Biológica Chamela of the Universidad Nacional Autónoma de Mexico near Chamela, Jalisco, Mexico (el. approximately 100 m —see Bullock 1988 for a detailed description of the habitat) during the first half of September in 1988, 1989, and 1990. Voucher

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specimens of both spiders and termites are deposited in the Museum of Comparative Zoology in Cambridge, MA 02138, USA, and in the collection of the Estación Biológica de Chamela.

The spiders are quite small (mature females are about 2–3 mm long), and their silk lines were generally not visible in the field. Positions of lines were deduced by lightly powdering them with cornstarch (which, unfortunately, often caused the spider to reel up the line it was on and replace it with another), and by noting the paths spiders took.

Experimental presentations of squashed termites and of clean forceps (as controls) involved the following protocol. One worker and one soldier were held together on the palm of my hand and squashed repeatedly with a watchmaker's forceps, then held for 60 s approximately 1 cm from the spider. Usually the squashed termites were slightly above the spider and, if possible without jarring vegetation or touching lines of silk, upwind of it. Since spiders generally hung upside down, the forceps and squashed termites were usually out of the spider's field of vision. Control presentations of forceps were similar in duration and position. The order of presentation was random, and approximately 1 min elapsed between each presentation. Unless otherwise noted, each spider was presented with only one control and one experimental stimulus. Statistical tests of significance employed two-tailed chi-squared tests.

RESULTS

Prey

107 spiders were found holding prey (some in the day and others at night) dangling on short lines under a leaf or twig 10–100 cm above the ground. All prey were worker or soldier termites. All identifiable (i.e., soldier) termites collected (on eight different days from in 1989 and 1990) were *Tenuirostritermes briciae*, an underground nesting species in which small parties of soldiers and workers forage on the forest floor for plant material which they cut into small pieces and carry underground. Foraging parties were apparently aboveground only briefly (in one timed case for only about 30 min; in other cases in which I did not see the termites first emerge, for at least 30, 60, 150, and 240 min) (on two occasions termites were driven back underground by ant attacks).

Tunnel openings were apparently generally not reused; in none of 40 cases in which I checked a site where I had seen foraging termites on a previous day were any termites on the surface. In all cases the openings had been sealed.

Relatively short trails (approximately 30–100 cm) which were up to about 1 cm wide connected the tunnel opening with the foraging site. Soldiers were mostly positioned at the periphery and faced outward, while workers were in more central areas. Soldiers were smaller than workers: the live weight of eight soldiers averaged 0.5 mg each, while that of 30 workers averaged 1.6 mg each.

Hunting and prey capture

The mystery of how a web-building spider captures wingless termites was answered by observations of more than 18 spiders hunting and capturing over 60 prey. Apparent searching behavior was performed by spiders found within 1 m of foraging parties of termites, and, less often, those away from termites. The spiders moved rapidly along more or less horizontal lines 1–15 cm above the leaf litter. The spiders often used lines already in place, but also frequently laid new lines by producing spanning lines (Eberhard 1987) carried on the breeze. Usually I could not see such new lines, but in two cases I saw a new line as it was emerging, and in five cases a new line was laid onto my body. Spiders also moved horizontally by shifting the attachments of lines they had already traversed, and then returning along the displaced lines. The spiders often moved quickly, and sometimes produced spanning lines with great rapidity.

An additional behavior, which was seen only within about 50 cm of foraging termites and was more certainly classified as searching behavior, consisted of quick, brief descents to the ground. Often, but not always, the spider paused 1 s or less on the ground, then always climbed back up its dragline, apparently without having attached a line to the ground. Occasionally a spider walked a short distance (<1 cm) along the ground before reascending its dragline. Descents of this type often occurred as the spider walked along a newly established horizontal line. Bursts of up to seven descents occurred in the space of 1 min. Descents seemed to be "blind" with respect to the location of the termites; in three cases a spider descended within 1 cm of the nearest termite, but then moved on and made descents farther away.

Nevertheless, the descents clearly functioned as searches, because when a descent brought a spider down onto a group of termites, its behavior changed abruptly and it began activities that culminated in attacks on prey. The spider did not attack the termite it had contacted, but instead immediately attached its dragline to the ground, and ran back up this more or less vertical line. Occasionally it descended to attach another line to the ground (e.g., Fig. 1). Usually (especially when its vertical line was not attached to a supporting object such as a leaf or twig directly above) it then ran along the horizontal line or lines to which the vertical line was attached until it reached or at least neared their ends—sometimes >30 cm away. After one or (usually) more such trips, the spider returned to the vertical line and descended along it. In one case in which the lighting and background were favorable, I saw that as the spider descended the horizontal line was pulled downward from about 4 cm to about 1 cm above the ground (Fig. 1). The spider spread its anterior legs as it neared the ground. Such "attack" descents were less rapid than the preceding "search" descents. Sometimes a spider made one or more additional attachments to the ground before making an attack descent. During attack descents spiders did not break the vertical line (deduced from subsequent events).

When the spider's spread legs encountered a termite (sometimes the spider waited for a termite to approach, other times it ran rapidly up to about 1 cm along the termite trail), the spider usually immediately grasped the dorsal surface of the prey. In 19 of 20 attacks by larger spiders and 3 of 3 by very small spiders which were observed carefully, the spider clasped the anterior half of the termite. The spider's chelicerae were generally positioned on the anterior portion of the termite's thorax. Attacks by very small spiders involved riding the termite for several seconds (maximum of 43 s in four timed attacks), while those of mature females were more rapid.

The termite's usual response to being attacked was to make violent and sustained rapid shaking or rocking movements forward and backward. Nearby termites sometimes showed brief interest in such struggles, but neither soldiers nor workers ever appeared to attack the spiders. The termite's struggles were generally ineffective against the spiders, as I only saw one of 65 attacked prey

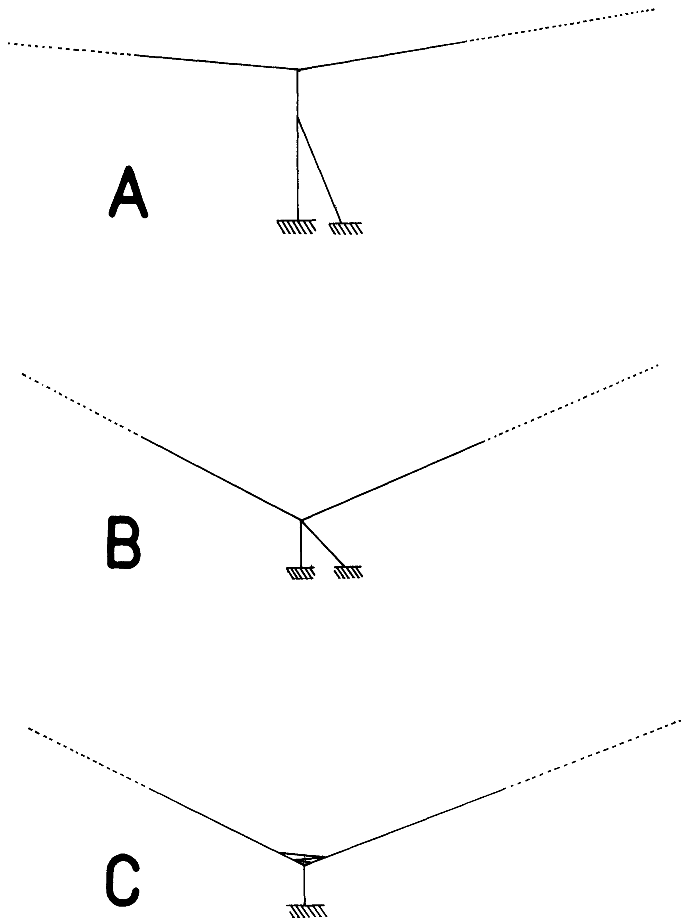

Figure 1. Diagrammatic representations of horizontal and vertical lines used by a mature female *Chrosiothes tonala* to attack termites. The horizontal line, which had been about 4 cm above the ground (A), was pulled downward (B) as the spider made its first attack descent. On the trip upward after capturing the first termite the spider made zig-zag attachments to the horizontal line (C), which probably resulted in the line becoming tighter.

escape. During these embraces the spider apparently both bit the termite (deduced from the fact that termites gradually became less active and eventually immobile without further contact with the spider), and attached its dragline to the termite (deduced from subsequent events) (neither behavior could be confirmed by direct observation).

During the first several attacks in a series by a larger spider, both the spider and the termite usually sprang 1–2 cm upward 1–5 s after the spider grasped the termite, and hung free on the end of the spider's dragline which was attached to a line above. This upward spring apparently resulted from tension on the spider's dragline (rather than tension on the vertical line), as the vertical line was not cut during these procedures. The spider immediately ran up the vertical line toward the horizontal line or the supporting object above, and apparently attached its dragline one or more times there. In one case I was able to see that on such a trip the spider made attachments on the arms of the "Y" formed by the vertical and horizontal lines (Fig. 1), thus apparently increasing the tensions on all three lines. Then it ran down the vertical line again to attack another termite. Usually the first 3–4 termites popped up off the substrate when attacked. Later prey remained in contact with the substrate, but were attached to a line leading upward. In some cases the spider made one or more return descents to a termite which had already been attacked, and in one case I saw that the spider rapidly wrapped silk (moved its hind legs alternately in a ventral direction in rapid succession—I could not see the silk lines it presumably produced) onto the anterior portion of the prey, then reascended and made one or more attachments above before descending again to launch another attack.

Small spiders usually attacked only a single termite before carrying it away to feed on it, while larger individuals captured up to more than 20 before carrying them off. The end of a series of attacks was signalled by descents to previously attacked prey which resulted in their releasing their holds on the substrate and being lifted off the ground. In at least two cases I could see that the spider apparently applied its mouthparts to one or more of the legs of the prey, and that this apparently caused the termite to release its hold on the substrate and to pop up off the substrate. The original vertical line to the substrate was also cut, and once all the termites hung free above the ground, the spider seized the line above them and began to carry the entire mass of prey upward and horizontally away from the termites on the ground. As it carried the prey mass away, the spider repeatedly descended to the captured termites. It attached lines to them which it then attached to other prey or to lines above, then climbed upward to attach its dragline to lines or objects further up. These attachments gradually caused the mass of prey to assume a more or less spherical shape. Sometimes the spider attached the line from which the mass hung to a support, floated new, more or less horizontal lines on the breeze, and then carried the mass along a new line dangling on the end of a line. After carrying the mass up to 1 m above the ground and 1 m horizontally, the spider attached the support line to an object (often the underside of a leaf), and began to feed.

Food masses were extraordinarily large compared with the spiders. For instances, two mature females which were captured as they carried off masses of prey weighed 1.4 and 1.2 mg; their prey masses weighed 28.2 and 29.9 mg respectively. Very small spiders, which weighed about 0.1 mg (11 spiders weighed 1.2 mg), likewise took prey up to >10 times their body weights (single soldiers and workers averaged 0.5 and 1.6 mg).

In an attempt to determine whether spiders were capturing extra prey to provide food for the future, termites in a mass of 10–12 workers captured <2 hrs previously were examined under a dissecting microscope. All but one were immobile and failed to respond to tactile stimulation; one leg of one individual twitched spontaneously. Another mass of newly captured prey taken from a spider before it began to feed was kept for two days in a vial with a green leaf (to maintain enough humidity to keep the termites alive); the termites became covered with fungus, suggesting that they had been killed by the spider. Sometimes feeding in the field lasted less than a day. On two occasions a recently captured prey mass was found <24 hours later abandoned by the spider (a third mature female was still on a prey mass 24 hours after first being sighted).

Prey specialization

Specialization of larger spiders on worker termites, and of smaller spiders on the smaller soldier caste was documented in two ways. Prey found captured by large spiders in nature tended to be workers, while those captured by smaller spiders tended to be soldiers (Table 1). In addition, direct observations of attacks by five mature females showed that on 16 occasions they contacted but failed to mount and bite a soldier termite, but attacked the next worker they touched. Similarly, three very small spiders were seen to touch but fail to attack five workers, and then attack the next soldier they contacted. Spiders sometimes rejected a prey after only very brief contact, so they may discriminate between workers and soldiers chemically.

How do spiders sense the presence of their prey?

Several lines of evidence suggest that the spiders use a chemical cue or cues to locate their prey. On one occasion I witnessed what was apparently the original emergence of a foraging party of termites aboveground, and saw that the three or four previously immobile spiders nearby suddenly began to hunt actively with both horizontal movements and repeated searching descents. The "blind" searching descents mentioned above which brought a spider to within less than 1 cm of a column of termites and which were followed by further descents farther away argue against the use of either visual or vibratory cues.

Hunting behavior was also induced by holding freshly squashed termites near spiders which were in the vicinity of foraging termites (Table 2). Test presentations to non-feeding immobile spiders not in the vicinity of foraging termites and in a small aquarium with leaf litter consistently failed to evoke searching descents, and usually failed to elicit any response whatsoever.

Table 1. Numbers of prey found in 1990 associated with different sized *Chrosiothes tonala* spiders feeding in the field (differences are highly significant, $p \ll 0.0001$). Spider sizes were estimated in the field: "small" includes the first and possibly the second instars outside the egg sac; "large" includes penultimate nymphs and adult females. Numbers in parentheses are numbers of spiders.

	Spider size		
Termite caste	*Small*	*Medium*	*Large*
Workers	21(20)	17(14)	251(34)
Soldiers	52(46)	3(2)	3(3)*

* All three large spiders that had captured a soldier had also captured several workers.

Table 2. Responses of spiders which were <0.5 m from foraging termites to the presentation of squashed termites (experimental) and clean forceps (control) held near them for 1 min. $\chi^2 = 8.4$, df = 2, $0.02 > p > 0.01$ comparing all three categories of behavior; $\chi^2 = 8.0$, df = 1, $0.01 > p > 0.001$ comparing searching descents vs. other behavior.

	Horizontal movement plus search descent	*Horizontal movement only*	*No reaction*
Experimental	12	6	5
Control	3	8	12

Egg sacs

Three spiders laid eggs in vials. Egg sacs were more or less spherical, and in two cases were under a label in the vial, suggesting that they may be laid under leaves (in the leaf litter?) in nature. Sacs were covered with a layer of relatively thick, curly, shiny lines that were very pale gold in color. Inside this cover a sphere layer of finer, white, more tightly curly lines could be seen. The sphere of non-agglutinate eggs was inside this.

Weights of three sacs and the spiders that produced them were 2.2, 0.9, and 2.9 mg, and 1.4, 1.3, and 1.3 mg respectively. Spiders thus produced sacs that were up to 69% of their own weight at the time of oviposition, a relatively high value when compared to those of related species (e.g., Eberhard 1979).

Other species utilizing termites captured by spiders

Female *Mycodiplosis* sp. (Cecidomyiidae) flies were seen on four different large masses of prey captured by mature females. In two cases the flies' abdomens were clearly swollen, so it appears that they fed on the termites. No interactions between the spiders and the flies were observed. In one further case a prey mass whose location had been marked 7 hrs earlier was found with the termites partially scattered on the leaf above, and a *Megaselia* sp. fly (Phoridae) apparently feeding on them.

On one occasion a salticid jumped onto a prey ball being fed upon by a mature female. The *C. tonala* spider escaped by falling on its dragline, but the salticid made off with the mass of prey.

Discussion

The consistent associations of *C. tonala* with captured *T. briciae* and no other prey, the complex and unusual attack behavior the spiders employ which is well-designed to capture termites, and the specialization of larger and smaller spiders on different termite castes all suggest that this spider may be a specialist on this termite. This is surprising in light of the fact that at least two other species in the genus *Chrosiothes* make aerial tangle webs with well-defined, highly ordered horizontal sheets (Eberhard unpub.).

It is still unclear whether the spiders are able to sense termite foraging parties from a distance and move toward them. The fact that sites where termites foraged for several hours "accumulated" up to 15 spiders with prey in an area of about 0.3 m^2 suggests that such long-distance movements may occur. On the other hand, the frequent, erratic changes in wind direction and the spiders' reliance on lines already laid or new lines (which can only be laid down-wind) would seem to make it difficult for them to perform such long-distance orientation. It is worth noting, however, that male spiders may often find females using airborne chemical cues, and thus may perform such feats routinely.

Foraging parties of the termites were not especially common (I typically found 1–2 in walking along 400–500 m of trail in the morning and checking a swath of about 1m in width). Presumably termites are more common in the vicinity of underground nests, but there is apparently no information on the foraging radius of *Tenuirostritermes* nests (Nutting 1970). Nutting et al. (1974) report repeated use of holes by foraging *T. tenuirostris*, but reuse of holes by *T. briciae* seems not to occur. I was unable to reliably spot *C. tonala* spiders in the field (a small individual resting under a leaf or stem was, for all intents and purposes, invisible), and thus could not document their distribution.

It is also not clear why spiders so often captured such huge masses of prey. The sizes of some egg masses were relatively large compared with the female spider's weight. The maximum weight of an egg sac (2.9 mg) still fell far short, however, of the weight of typical prey bundles of adult females (up to 29.9 mg). Termites apparently died soon after being captured, and spiders in the field abandoned some prey masses within less than a day, so it does not appear that the spiders were capturing extra prey in order to keep them for future use. Perhaps spiders capture more prey than they can possibly utilize in order to be certain not to suffer negative effects from the kleptoparasitic cecidomyiid flies. Or perhaps spiders are only able to utilize a small fraction of each termite as food.

There are several problems in interpreting the results of the experiments with squashed termites (it was not clear when and if the odor actually reached the resting spider; some spiders were unresponsive and uninterested in hunting). Nevertheless the combination of the results of these experiments and the several indirect indications from undisturbed attack behavior make it seem likely that spiders use chemical cues to find termites. Although it is tempting to suppose that the chemicals involved are the same as those used by the termites themselves to coordinate their movements, there is as yet no evidence on this point. Other predators, such as the reduviid *Apiomerus pictipes*, apparently use pheromones of their prey (Johnson 1983).

Summary

Chrosiothes tonala spiders captured *Tenuirostritermes briciae* termites foraging on the forest floor, using searching behavior that included repeated descents to the ground, and attacks involving a simple spring web made on the spot after having contacted the prey. The spiders probably used chemical cues from the termites to release active searching behavior, and perhaps to guide searches for prey. Early instar spiders usually captured soldier termites, while larger spiders captured almost exclusively the larger workers. There was a positive correlation between spider weight and weight of termites captured, and mature females captured up to more than 24 times their body weight of termites in a single series of attacks. At least three other arthropod species (a cecidomyiid fly, a phorid fly, and a salticid spider) fed on masses of termites captured by *C. tonala*.

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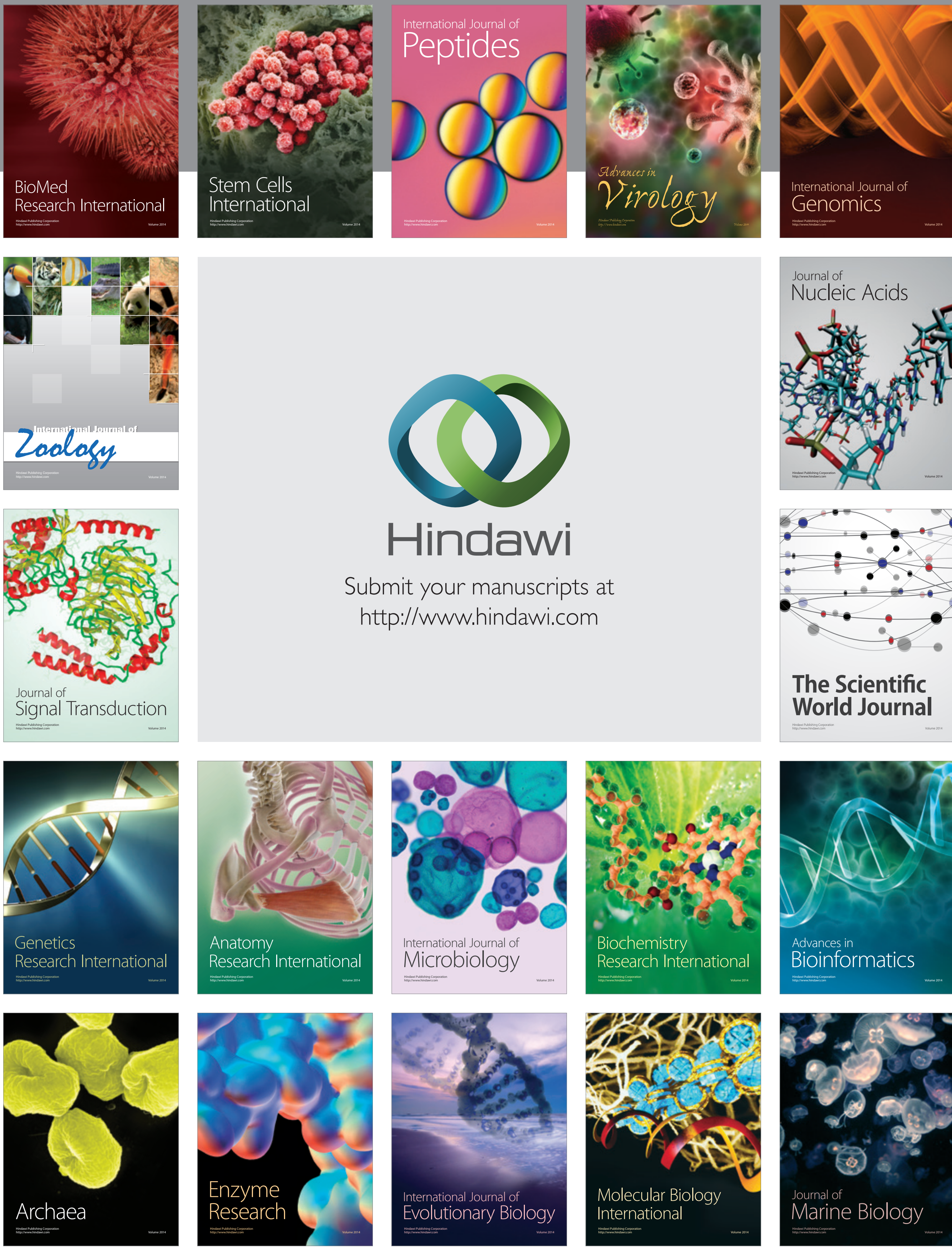
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