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Original Article

Antennal sensilla morphology of *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae), a larval parasitoid of the maize weevil, *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae)

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ABSTRACT

The antennal sensilla of *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae), a larval parasitoid of the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) were investigated using scanning electron microscopy. The antennal sensilla of female and male wasps appeared similar in shape and types. Antennal sensilla in female and male *T. elegans* were classified into four groups: basiconic capitate peg sensilla, chaetica sensilla (types 1–5), placoid sensilla and trichoid sensilla. Chaetica sensilla type 5 were found only on the female antenna. These four groups of antennal sensilla probably function as proprioceptors, hygro- and thermo- mechanoreceptors or contact chemoreceptors. The receptors are involved in host examination, host discrimination, host recognition and host location by female and male *T. elegans*.

Introduction

The suitability of parasitoids for stored-product insect pest control depends on certain characteristics (Steidle and Schöller, 2002). The success of parasitoids in suppressing stored-product insect pest populations depends on their ability to locate hosts – a process with parasitoids that is hierarchical involving host-habitat location, host location and host acceptance (Godfray, 1994; Quicke, 1997). The chemoreceptors which play a role in host finding may be specific in location on the antenna of parasitoids (Norton and Vinson, 1974; Germinara et al., 2009). The antennae of female parasitic Hymenoptera are involved in habitat searching, host location, host examination, host recognition, host acceptance, oviposition, host discrimination and mating behavior (Godfray, 1994; Quicke, 1997).

Theocolax elegans (Westwood) (Hymenoptera: Pteromalidae) is a solitary larval ectoparasitoid of stored-product insect pests such as the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae). Several studies have examined the potential of this parasitoid for suppressing stored-product insect pests in biological control programs (van den Assem and Kuenen, 1958; Williams and Floyd, 1971; Press, 1992; Pacho, 1993; Ryoo et al., 1996; Toews et al., 2001; Flinn and Hagstrum, 2001, 2002; Hayashi et al., 2004; Flinn et al., 2006; Uraichuen et al., 2006; Yan et al., 2006; Dlamini and Amornsak, 2014).

Several studies have examined the antennal sensilla of various species of parasitic wasps using electron microscopy (Slifer, 1969; Norton and Vinson, 1974; Amornsak et al., 1998; Xiao and Huang, 2001; Gao et al., 2007; Dweck and Gadallah, 2008; Onagbola and Fadamiro, 2008; Dweck, 2009; Doganlar and Doganlar, 2010; Obonyo et al., 2011; Li et al., 2012, 2013; Ruschioni et al., 2012; Zhou et al., 2015). Several pteromalid wasp studies have reported details on the external morphology and "types" of antennal sensilla (Slifer, 1969; Xiao and Huang, 2001; Onagbola and Fadamiro, 2008; Dweck, 2009). However, *T. elegans* requires more information concerning the external morphology of the antennal sensilla. The current study focused on the antennal sensilla associated with the host-habitat and host-finding abilities of a parasitoid that may be important to stored-product insect pest management.

The study investigated the external morphology of the antennal sensilla of *T. elegans* using scanning electron microscopy (SEM), and suggests investigated the function and possible roles of the sensilla types in this parasitic wasp.

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Materials and methods

Insect

T. elegans and *S. zeamais* were received from the Office of Research and Development on Post-harvest and Processing, Department of Agriculture, Bangkhen, Bangkok, Thailand. One pair of *T. elegans* was used to establish a single "pure line" colony. *S. zeamais* was reared on brown rice as a host substrate. Twenty-one day-old *S. zeamais* larvae were provided to *T. elegans* neonate mated females for oviposition. *T. elegans* adults were fed with honey. Stock culture of *T. elegans* and *S. zeamais* were maintained at the National Biological Control Research Center, Headquarters, Kasetsart University, Bangkhen campus, Bangkok, Thailand under laboratory conditions of 26 °C, 60% relative humidity and 12 h light: 12 h darkness photoperiod.

Scanning electron microscopy

Female and male wasps were killed and cleaned with liquid detergent. Then, the wasps were rinsed twice with distilled water. Wasps were first fixed in 2.5% glutaraldehyde in 0.2 M phosphate buffer at pH 7.2 for 12 h after which the specimens were rinsed twice with distilled water. Post-fixation was prepared in 1% osmium tetroxide for 1 h. Subsequently, the specimens were washed in distilled water. The specimens then were dehydrated in a graded ethyl alcohol series. Next, the specimens were critical-point dried and mounted on aluminum stubs using double-sided sticky tape. A scanning electron microscope (JSM 5600 LV; JEOL; Tokyo, Japan) operated at 10 kV was used to observe the antennal sensilla which were classified on the basis of their size and shape.

Terminology

The current study defined the antennal sensilla following the terminology of Amornsak et al. (1998). Abbreviations used in this paper are: C = club, F = funicle, A = anellus, P = pedicel, Sc = scape, R = radical, BCPS = basiconic capitate peg sensilla, ChS = chaetica sensilla, PS = placoid sensilla, TS = trichoid sensilla.

Statistical analysis

The sensilla on the surfaces of the antennae of *T. elegans* were classified and measured. Basic descriptive statistics (mean ± SD) were determined using Microsoft Excel (2007; Microsoft; Redmond, WA, USA).

Results

Antennae of T. elegans

The antennae of *T. elegans* consist of a scape with radicula, pedicel, anellus and the flagellum is divisible into a funicle and club as shown in Fig. 1.

The female antenna is geniculate. The radical is separated from the scape and positioned in the socket. Each segment of the antenna has different types of sensilla. The flagellum consists of an anellar segment, 5–6 funicular segments and a one-segmented club. The anellus is small, ring-like and can more clearly be seen on male antenna than female antenna of *T. elegans* (Fig. 2). The funicular segments are cylindrical and the club segment is barrel-shaped. Both sexes display a furrowed surface.

The mean length of the antennal segments in males and females are summarized in Table 1.

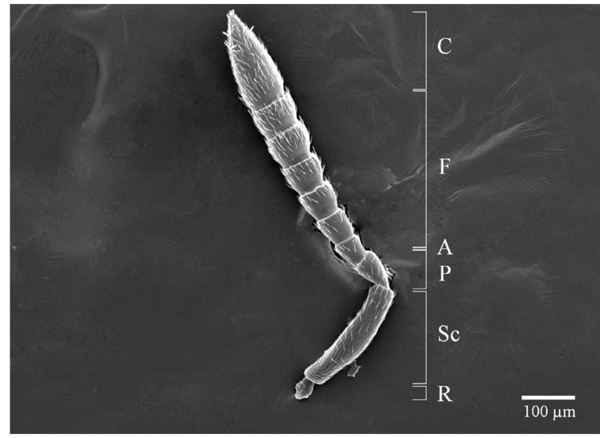

Fig. 1. Scanning electron photomicrograph of female *Theocolax elegans* antenna (C = club, F = funicle, A = anellus, p = pedicel, Sc = scape, R = radicula).

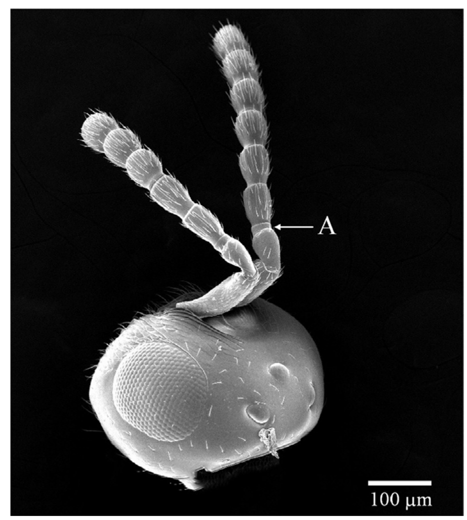

Fig. 2. Scanning electron photomicrograph showing the male anellus (A) on the antenna of *Theocolax elegans.*

Table 1
Length (mean ± SD) of antennal segments in female and male *Theocolax elegans*.

	Antennal segment	
	Female (µm)	Male (µm)
Scape	226.67 ± 92.34	192.76 ± 37.41
Pedicel	99.49 ± 67.81	75.48 ± 19.49
Flagellum	475.44 ± 174.34	411.62 ± 91.24
Total	801.58 ± 55.79	679.86 ± 37.35

The sensilla of male and female *T. elegans* may be classified into eight different types, based on their size, shape, cuticular surface and basal socket. The sensilla are: basiconic capitate peg sensilla, chaetica sensilla (types 1–5), placoid sensilla and trichoid sensilla.

Basiconic capitate peg sensilla

Basiconic capitate peg sensilla are distinguished by their structure and cuticular surface. They are bulb-like structures, pegs with grooves along the bulb, 3.5 ± 0.43 µm long and set into a shallow cuticular depression (Fig. 3A). Six BCPS occur on the distal part of

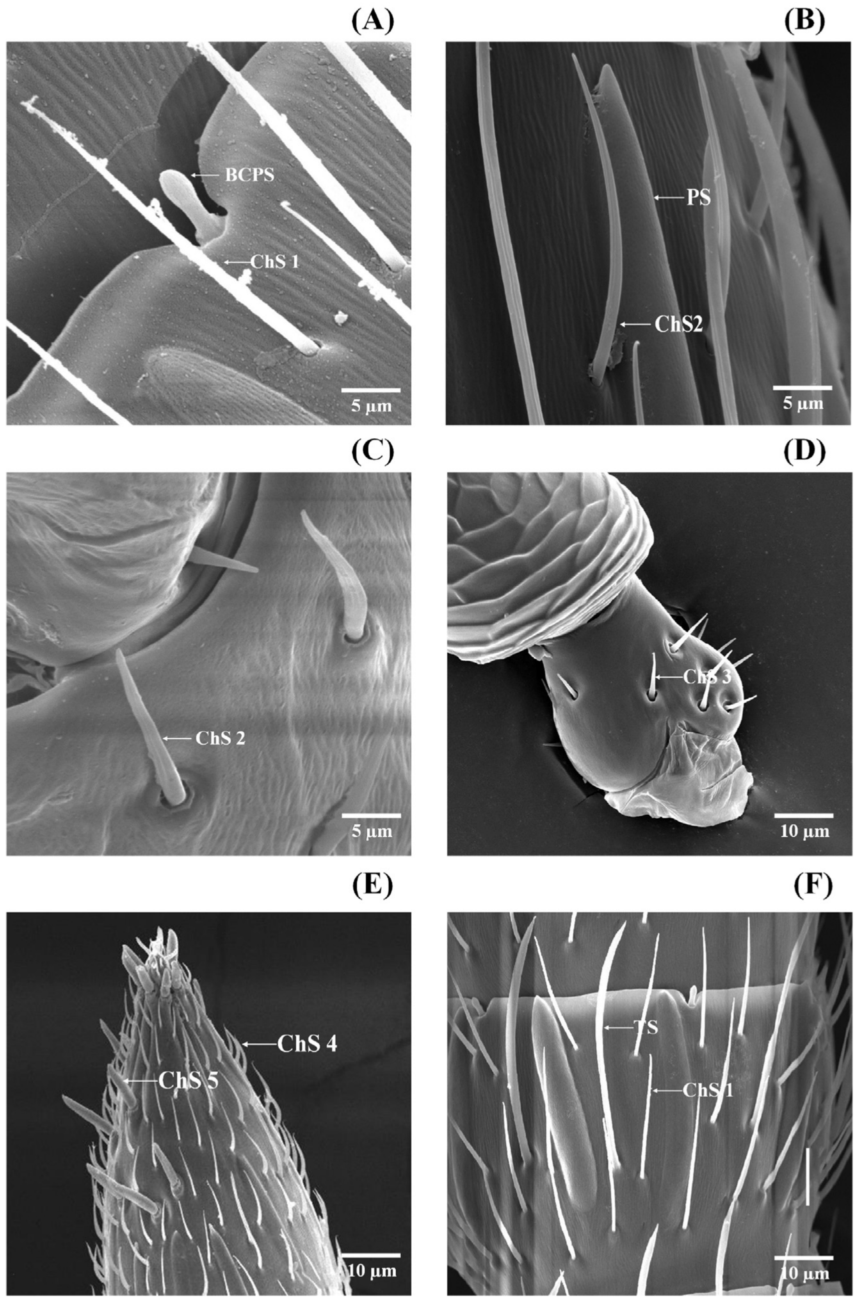

Fig. 3. Scanning electron photomicrographs of *T. elegans* antennae: (A) BCPS = basiconic capitate peg sensilla, ChS 1 = chaetica sensilla, type 1; (B, C) PS = placoid sensilla, ChS 2 = chaetica sensilla, type 2; (D) ChS 3 = chaetica sensilla, type 3; (E) ChS 4 = chaetica sensilla, type 4; ChS 5 = chaetica sensilla, type 5; (F) TS = trichoid sensilla.

funicle segments 4–6 in both female and male antennae and occur only on the club on female antennae.

Chaetica sensilla

Chaetica sensilla are classified by their cuticular surface, shape and basal socket. Five types of ChS occur on antennae of *T. elegans*. Chaetica sensilla, type 1 (ChS 1) are elongate, slender, apically pointed, 11.37 ± 1.04 μm long and set into a small conical basal socket (Fig. 3A and F). ChS 1 occur on the scape, pedicel, funicle and club in both female and male antennae. ChS 1 vary in length and basal socket depending on their location on the antennae. Chaetica sensilla, type 2 (ChS 2) are elongate, slender with pointed apices, 11.32 ± 0.84 μm long and show a deep basal insertion into sockets (Fig. 3B and C). ChS 2 have a few grooves on the cuticular surface. ChS 2 occur on the scape, pedicel, funicle and club of male and female antennae *T. elegans*. ChS 2 vary in length and basal socket depending on their location on the antennae. Chaetica sensilla, type 3 (ChS 3) are relatively short and insert into large pits. Each ChS 3 sensillum is triangular, peg-like with a smooth surface, pointed apex and 6.75 ± 1.20 μm long (Fig. 3D). ChS 3 occur on the basal portion of the radicula. Chaetica sensilla, type 4 (ChS 4) are relatively short, slender, 9.12 ± 0.69 μm long and set into the socket. ChS 4 have a smooth surface and are curved (Fig. 3E). ChS 4 occur on the club and appear in rows on the lateral aspect of the club in female antenna. Chaetica sensilla, type 5 (ChS 5) have a smooth surface with blunt apices, 7.03 ± 1.70 μm long and are set into the socket (Fig. 3E).

ChS 5 seem more stout than slender. ChS 5 occur on the distal part of the female antenna.

Placoid sensilla

Placoid sensilla are the largest sensilla type on the antennae of *T. elegans*. They are 39.9 ± 1.43 μm long elongate plate-like sensory organs with shafts containing numerous. Each sensillum arises from an elevated cuticular rim and tapers apically (Fig. 3B). PS occur on all funicular segments and the club on both female and male antennae of *T. elegans*.

Trichoid sensilla

Trichoid sensilla are relatively long (42.35 ± 2.14 μm) and tapering but have no socket. Each sensillum arises from the cuticle and has a smooth surface (Fig. 3F). TS occur on the funicular and club on both female and male antennae of *T. elegans*.

Discussion

The current study revealed eight morphologically different types of sensilla on the antennae of female and male *T. elegans*. These sensilla are consistent with descriptions of other pteromalid species including: *Nasonia vitripennis* (Slifer, 1969), *Angulifrons reticulata* sp. n. (Xiao and Huang, 2001), *Rhopalicus tutela* (Petterson et al., 2001), *Pteromalus cereallae* (Onagbola and Fadamiro, 2008) and *Pteromalus puparum* (Dweck, 2009) as well as other Hymenoptera parasitoids such as: *Melittobia australica* (Eulophidae) (Dahms, 1984), *Epidinocarsis lopezi* and *Leptomastix dactylopii* (Encyrtidae) (van Baaren et al., 1996), *Trichogramma australicum* (Trichogrammatidae) (Amornsak et al., 1998), *Cotesia sesamia* and *Cotesia flavipes* (Braconidae) (Obonyo et al., 2011), *Quadrastichus erythrinae* (Eulophidae) (Li et al., 2013) and *Sclerodermus* sp. (Bethylidae) (Zhou et al., 2015) as shown in Table 2.

The current study found that the antennal sensilla in female and male *T. elegans* can be classified into four groups: basiconic capitate peg sensilla, chaetica sensilla types 1–5, placoid sensilla and trichoid sensilla.

The basiconic capitate peg sensilla in *T. elegans* resemble other pteromalid species and other parasitoids with little difference in terminology as shown in Table 2 (Dahms, 1984; van Baaren et al., 1996; Amornsak et al., 1998; Xiao and Huang, 2001; van Baaren et al., 2007; Onagbola and Fadamiro, 2008; Dweck, 2009; Obonyo et al., 2011; Li et al., 2013; Zhou et al., 2015). The other terminology includes "coeloconic sensillum" in *R. tutela* (Petterson et al., 2001). The position and structure of BCPS can be suggested to have an olfactory function or as hygro-, thermo- and mechanoreceptors (Dahms, 1984; van Baaren et al., 1996; Amornsak et al., 1998; van Baaren et al., 2007; Onagbola and Fadamiro, 2008; Dweck, 2009; Li et al., 2013; Obonyo et al., 2011; Zhou et al., 2015).

Chaetica sensilla are the most abundant sensilla found in *T. elegans* and can be classified by the cuticular surface and basal socket. The current study differentiated ChS and TS by the presence or absence of a socket (Amornsak et al., 1998). Chaetica sensilla types 1–4 appear on the radicula, scape, pedicle and club on both the female and male antennae of *T. elegans*.

The distribution and location of ChS are the key to defining the role of the antennal sensilla of *T. elegans*, which are related to previously described sensilla in other pteromalid species (Table 2) including the "sensilla chaetica type 1" in *C. sesamia* and *C. flavipes* (Obonyo et al., 2011) and "sensilla trichodea type 1" in *Sclerodermus* sp. (Zhou et al., 2015). ChS 1 occur on the scape, pedicel, funicle and club on the female and male antennae of *T. elegans*, similar to the reports on all species that have been cited. These sensilla probably have a mechanoreceptor function and detect changes of antennal position on the scape and pedicel (Amornsak et al., 1998; Onagbola and Fadamiro, 2008; Li et al., 2013; Zhou et al., 2015).

Chaetica sensilla, type 2 of *T. elegans* resemble other pteromalid species and other parasitoids (Table 2) including the "sensilla chaetica type 2" in *L. dactylopii* (van Baaren et al., 1996), and "sensilla trichodea type 2" in *Sclerodermus* sp. (Zhou et al., 2015). ChS 2 are distributed as ChS 1 in *T. elegans*. These sensillum types can be assigned a mechanoreceptor function (Amornsak et al., 1998; Onagbola and Fadamiro, 2008; Li et al., 2013; Zhou et al., 2015). Due to their location on the club of ChS 2 in *T. elegans*, Onagbola and Fadamiro (2008) suggested that these sensilla may be involved in host examination during antennal drumming behavior.

Chaetica sensilla, type 3 in *T. elegans* resemble other pteromalid species and other parasitoids (Table 2). By their position and shape, ChS 3 occur on the basal portion of the radicula. It was assumed that these sensilla function as proprioceptors (Amornsak et al., 1998; Onagbola and Fadamiro, 2008).

Chaetica sensilla, type 4 of *T. elegans* resemble other pteromalid species and include "short, curved tactile hair" in *N. vitripennis* (Slifer, 1969), and the "sensilla trichodea type 3" in *Sclerodermus* sp. (Zhou et al., 2015). ChS 4 occur on the club and appear in rows on the lateral aspect of the club in female *T. elegans*. By the position and shape of ChS 4, it was assumed they had gustatory and mechanosensory functions, which play an important role in host discrimination (Van Baaren et al., 1996).

Chaetica sensilla, type 5 have a unique structure in *T. elegans*. ChS 5 resemble other pteromalid species and other parasitoids (Table 2) including the "thick walled chemoreceptor" in *N. vitripennis* and "sensilla chaetica type 4" in *E. lopezi* and *L. dactylopii* (van Baaren et al., 1996). The position of ChS 5 in female *T. elegans* antennae can be described as "contact chemoreceptors"

Table 2
Comparison of terminologies in antennal sensilla types of *Theocolax elegans* and other parasitoids.

Hymenoptera parasitoids	Pteromalid species			Other parasitoids	
Sensilla types of *Theocolax elegans*	*Angulifrons reticulata* sp. n. (Xiao and Huang, 2001)	*Pteromalus cereallae* (Onagbola and Fadamiro, 2008)	*Pteromalus puparum* (Dweck, 2009)	*Trichogramma australicum* (Amornsak et al., 1998)	*Quadrastichus erythrinae* (Li et al., 2013)
Basiconic capitate peg Sensilla	Basiconic capitate peg	Basiconic capitate peg sensilla	Basiconic capitate peg sensilla	Basiconic capitate peg sensilla	Basiconic capitate peg sensilla
Chaetica sensilla, type 1	Slender, sharp-tipped hair	Aporous type 1 sensilla trichodea	–	Chaetica sensilla, type 1	Chaetica sensilla II
Chaetica sensilla, type 2	–	Aporous type 2 sensilla trichodea	Nonporous sensilla trichodea type 1	Chaetica sensilla, type 2	Chaetica sensilla I
Chaetica sensilla, type 3	–	Aporous type 4 sensilla trichodea	Nonporous sensilla chaetica	Chaetica sensilla, type 3	–

and may be involved in host recognition (van Baaren et al., 1996; Onagbola and Fadamiro, 2008; Dweck, 2009).

Placoid sensilla in *T. elegans* resemble other pteromalid species and other parasitoids with little difference in terminology as shown in Table 2 (Dahms, 1984; van Baaren et al., 1996; Amornsak et al., 1998; van Baaren et al., 2007; Onagbola and Fadamiro, 2008; Dweck, 2009; Li et al., 2013; Obonyo et al., 2011; Zhou et al., 2015). The other terminology includes "plate organ" in *N. vitripennis* (Slifer, 1969). The multiple pores of PS suggest an olfactory function, which may play a role in host location and the detection of host-related semiochemicals (Amornsak et al., 1998; Onagbola and Fadamiro, 2008; Dweck, 2009).

Trichoid sensilla in *T. elegans* resemble other pteromalid species and other parasitoids with little difference in terminology as shown in Table 2 (Dahms, 1984; van Baaren et al., 1996; Amornsak et al., 1998; Petterson et al., 2001; Li et al., 2013). The other terminology includes "thin-walled chemoreceptors" in *N. vitripennis* (Slifer, 1969). TS are mainly mechanosensory but some are also chemosensory (Quicke, 1997; Amornsak et al., 1998; Dweck, 2009) and Petterson et al. (2001) reported that the sensilla trichodea could function as pheromone receptors in *R. tutela*.

The antennae of female and male *T. elegans* appear similar, geniculate in shape, 801.58 ± 55.79 μm long in the female and 679.86 ± 37.35 μm long in the male. The current study revealed eight morphologically different types of sensilla on the antennae of female and male *T. elegans*, which could be classified into four groups: basiconic capitate peg sensilla, chaetica sensilla (types 1–5), placoid sensilla and trichoid sensilla. Basiconic capitates peg sensilla occur on the distal part of the funicle segments; these sensilla may have an olfactory function or as hygro-, thermo- and mechanoreceptors. Chaetica sensilla types 1 and 2 occur on scape, pedicel, funicle and club on female and male antennae; ChS 1 and ChS 2 can be assigned as mechanoreceptors. ChS 3 occur on the basal portion of the radicula and ChS 3 may be proprioceptors. ChS 4 occur on the club on female and male antennae. It was assumed that ChS 4 have gustatory and mechanosensory functions. ChS 5 occur on the distal part of the female's antennal club and can be described as contact chemoreceptors. Placoid sensilla occur on all funicular segments. The multiple pores of PS suggest an olfactory function. Trichoid sensilla occur on the funicular segment and club and TS are mainly mechanosensory. However, some are also chemosensory and these sensilla are assumed to act as pheromone receptors. Collectively, these four groups of antennal sensilla are involved in host examination, host discrimination, host recognition and host location of female and male *T. elegans*.

This study interpreted basic information on the external morphology and antennal sensillum types of *T. elegans*, which can lead to further studies of the antennal sensilla of *T. elegans*.

Conflict of interest

There is no conflict of interest.

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