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# Stalk-eyed wasps—review of a largely unnoticed group of morphologically bizarre chalcidoid wasps (Hymenoptera: Eurytomidae: *Axima*)

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## Abstract

*Axima* Walker is a small genus of Eurytomidae (Hymenoptera: Chalcidoidea) exclusive to the Western Hemisphere. Some species are distinctive in having stalked eyes and *Axima sidi*, **sp. n.** is described as the third stalk-eyed species based on a single female from Colombia. A key to facilitate species identification of stalk-eyed *Axima* is included. The only species of *Axima* for which host biology is known is a primary parasitoid of dwarf carpenter bees of the genus *Ceratina* Latreille (Apidae: Xylocopinae). A hypothesis about the possible function of stalked eyes in *Axima* as devices to assist the escape of adult wasps from hosts enclosed in the soft pith of plant stems is proposed.

**Key words:** Colombia, new species, functional morphology, Chalcidoidea

## Introduction

Stalk-eyed species are known from various insect groups, including Diptera (e.g., Diopsidae, Drosophilidae, Platystomatidae), Coleoptera (Anthribidae: males of *Exechesops* spp.) and Heteroptera (e.g., Lygaeidae, Malcidae). The stalk-eyed condition in these insects is characterized by a unique head expansion into dorsolateral processes, which carry the compound eyes. Within Hymenoptera, this extreme form of head modification was so far only known from two morphologically bizarre species of Eurytomidae (Chalcidoidea), which were described independently from each other about 35 years ago and since then have received little attention. The description of *Axima noyesi* Subba Rao was published in December 1978 and that of *Aplatoides diabolus* Yoshimoto & Gibson just four months later in April 1979. Even though the species were described in different genera, they are closely related and today classified in *Axima* Walker (Lotfalizadeh *et al.* 2007). Here, we propose the common name "stalk-eyed wasps" for this unique group of Hymenoptera and describe a third species from Colombia. A possible tool-function of the stalked eyes during emergence from hosts is briefly discussed.

## Material and methods

The newly described species was obtained as a result of a collaborative collecting effort in Colombia. The Amacayacu National Park was one of 31 natural areas throughout Colombia chosen for an intensive survey of Hymenoptera under the project "Insect Survey of a Megadiverse Country, Phase I & II: Colombia" ["Diversidad de Insectos de Colombia"]. Morphological terminology follows the Hymenoptera Anatomy Ontology (Hymenoptera Anatomy Consortium 2014). Images were taken with a Leica DXM 1200 digital camera attached to a Leica MZ 16 APO microscope and processed using AutoMontage (Syncroscopy) software and post-processed with Adobe Photoshop CS5.1. The following abbreviations are used in the text: cl = clava, F = flagellomere, fp = frontal projection, msc = mesoscutal carina, Mt = metasomal tergite, ped = pedicel, pi = pronotal invagination, PNN = Parque Nacional Natural, ssc = mesoscutellar carina.

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## Systematics

### Eurytomidae Walker, 1832

### Eurytominae Walker, 1832

### *Axima* Walker, 1862

*Axima* Walker, 1862: 373. Type species, *Axima spinifrons* Walker, 1862, by monotypy.
*Aplatoides* Yoshimoto & Gibson, 1979: 421. Type species, *Aplatoides diabolus* Yoshimoto & Gibson, 1979, by original designation. [Synonymy by Lotfalizadeh *et al.* (2007).]

**Diagnosis.** Head distinctly broader than mesosoma and with small denticle or large projection on vertex laterally between scrobal depression and eye. Eye protruding, sometimes situated on tubular process. Face with interantennal region distinctly truncate. Anterior ocellus above scrobal depression. Gena carinate laterally. Anterior margin of pronotum carinate laterally; dorsomedially rounded with raised sculpture close to anterior pronotal margin, sometimes forming distinct spine. Dorsal surface of propodeum lying at approximately 45° angle with longitudinal axis of thorax. Propodeum extending beyond bases of metacoxae. Metasoma with long, slender petiole, and with compressed, smooth, lanceolate gaster having Mt2–Mt4 reduced and often patches of white setae on remaining terga (Walker 1862, Burks 1971, DiGiulio 1997).

**Comments.** Eight species of *Axima* are known, including the new species described herein, which are restricted to the New World (Table 1). Only three of these are characterized by stalked eyes, a unique morphological modification that led Yoshimoto & Gibson to establish a separate genus for *A. diabolus*. Lotfalizadeh *et al*. (2007) recognized *A. diabolus* as a derived species within *Axima* and synonymized the name *Aplatoides* under *Axima*. So far no male stalk-eyed wasps have been found. Based on the results of a phylogenetic analysis of morphological characters, Lotfalizadeh *et al.* (2007) proposed seven autapomorphies of *Axima*: (1) head transverse in frontal view, with protruding eyes; (2) lateral foraminal plate completely delimited laterally; (3) postgenal bridge without median stripe of ornamentation, and only a few digitiform expansions visible; (4) propodeum with elongate nucha; (5) metapleuron with ventral shelf very long; (6) petiole elongate and bent downwards posteriorly; and (7) Mt5 long. Initially, *Axima* was placed in the subfamily Aximinae, but this is now considered a synonym of Eurytominae (Stage & Snelling 1986). Currently, *A. zabriskiei* Howard is the only species for which biological information is associated. This species has been reared as solitary or gregarious ectoparasitoids of dwarf carpenter bees of the genus *Ceratina* Latreille, subgenus *Zadontomerus* Ashmead (Apidae: Xylocopinae) (Howard 1890, Rau 1928, Krombein 1960, Peck 1963, Burks 1966, Kislow 1976). The larval development was studied by Burks (1966).

The morphological distinctiveness of stalk-eyed wasps led us to treat them here in an informal species group within *Axima*, i.e., the *noyesi* species group (=*Aplatoides*, see Yoshimoto & Gibson 1979 for an extensive diagnosis) and treat the remaining species in the *spinifrons* species group.

### Key to females of *Axima noyesi* species group

1 Head produced dorsolaterally into tubular process bearing eye at apex . . . . . . . . . . . . . . . . . . . . . . . .(*noyesi* species group) …2
- Head not produced dorsolaterally into tubular process, eye in normal position . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .(*spinifrons* species group, see key in Ashmead 1904, pp. 458–459)
2 Mesoscutum without median carina. Mesoscutellar process dorsally pointed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*A. diabolus* (Yoshimoto & Gibson, 1979, fig. 3)
- Mesoscutum with median carina at least slightly indicated. Mesoscutellar process dorsally rounded (Fig. 2) . . . . . . . . . . . . . . 3
3 Median mesoscutal carina slightly indicated (Fig. 8), laterally flanked by rows of piliferous punctures (rounded depressions). Mt5 and Mt6 with distinct setation (Fig. 10). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. noyesi* Subba Rao, 1978
- Median mesoscutal carina more distinctly raised (Fig. 7), laterally flanked by rows of piliferous foveae (subrectangular depressions). Mt5 bare, Mt6 with few scattered setae (Fig. 9). . . . . . . . . . . . . . . . . . . . . *A. sidi* Arias-Penna, Pape & Krogmann, **sp. n.**

**TABLE 1.** Checklist of *Axima* species.

| Species group | *Axima* species | Distribution | References |
|---|---|---|---|
| *spinifrons* "normal-eyed wasps" | ***A. brasiliensis*** Ashmead, 1904 | Brazil: Pernambuco (Bonito)<br>Colombia: Norte de Santander (San Alberto) | Ashmead 1904<br>Lotfalizadeh *et al.* 2007 |
| | ***A. brevicornis*** Ashmead, 1904 | Brazil: Bahía (Chapada Diamantina National Park), Mato Grosso do Sul (Corumbá), Pará (Santarém)<br>Colombia: Norte of Santander (San Alberto) | Ashmead 1904<br>Lotfalizadeh *et al.* 2007 |
| | ***A. koebelei*** Ashmead, 1904 | Brazil: Pernambuco (Bonito)<br>Argentina | Ashmead 1904<br>De Santis 1979 |
| | ***A. spinifrons*** Walker, 1862 | Brazil: São Paulo (São Paulo) | Walker 1862<br>Ashmead 1904 |
| | ***A. zabriskiei*** Howard, 1890 | Canada (Quebec)<br>U.S.A (California, Indiana, Michigan, Missouri, New Jersey, New York, Texas, Virginia, West Virginia) | Howard 1890<br>Peck 1963<br>Burks 1979<br>Noyes 2014 |
| *noyesi* "stalk-eyed wasps" | ***A. sidi*** Arias-Penna, Pape & Krogmann, **sp. n.** | Colombia: Amazonas (Puerto Nariño, PNN Amacayacu) | |
| | ***A. diabolus*** (Yoshimoto & Gibson, 1979) | Brazil: Goiás (Jataí) | Yoshimoto & Gibson 1979 |
| | ***A. noyesi*** Subba Rao, 1978 | Trinidad and Tobago: Tunapuna-Piarco (Saint George, Arena forest Reserve) | Subba Rao 1978 |

## Description of new species

### *Axima sidi* Arias-Penna, Pape & Krogmann, sp. n.

(Figs 1–7, 9)

**Type material.** Holotype female: Colombia, Amazonas, PNN Amacayacu, San Martín, 3°46'S 70°18'W 150 m, sweepnet, 01–10.iii.2004, T. Pape & D. Arias leg. M.4327, IAvH-80813. The holotype is deposited in Instituto de Investigación en Recursos Biológicos Alexander von Humboldt (IAvH), Villa de Leyva, Boyacá, Colombia.

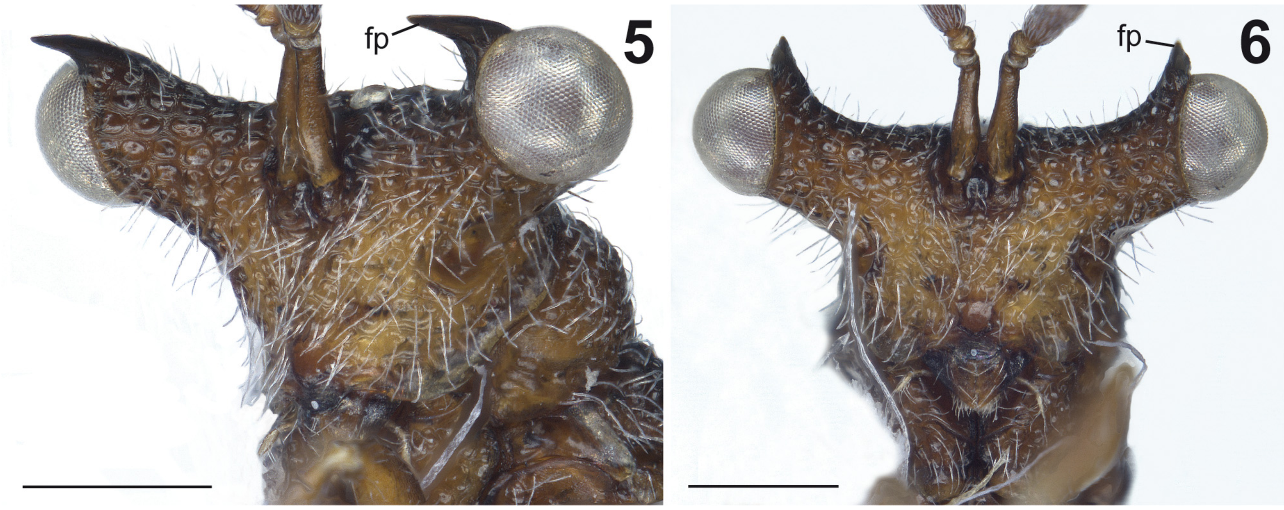
**Diagnosis.** Median mesoscutal carina (Figs 2, 7) distinctly raised, laterally flanked by rows of piliferous foveae. Mesoscutellar process distinctly higher than level of mesoscutum, dorsally rounded. Metasomal terga without distinct white setation (Figs 1, 9), Mt5 bare, Mt6 with few scattered setae (Fig. 9).

**Description.** Body color (Figs 1–7, 9). Body generally brown with ventral and lateral portions of head (Figs 5, 6), mesosoma (Figs 1, 2, 7) and metasoma (Figs 1, 9) yellowish-brown. Legs yellowish brown (Fig. 1). Fore and hind wings hyaline except region immediately below submarginal vein very slightly infumate. Body length: 5.90 mm, head plus mesosoma: 2.35 mm.

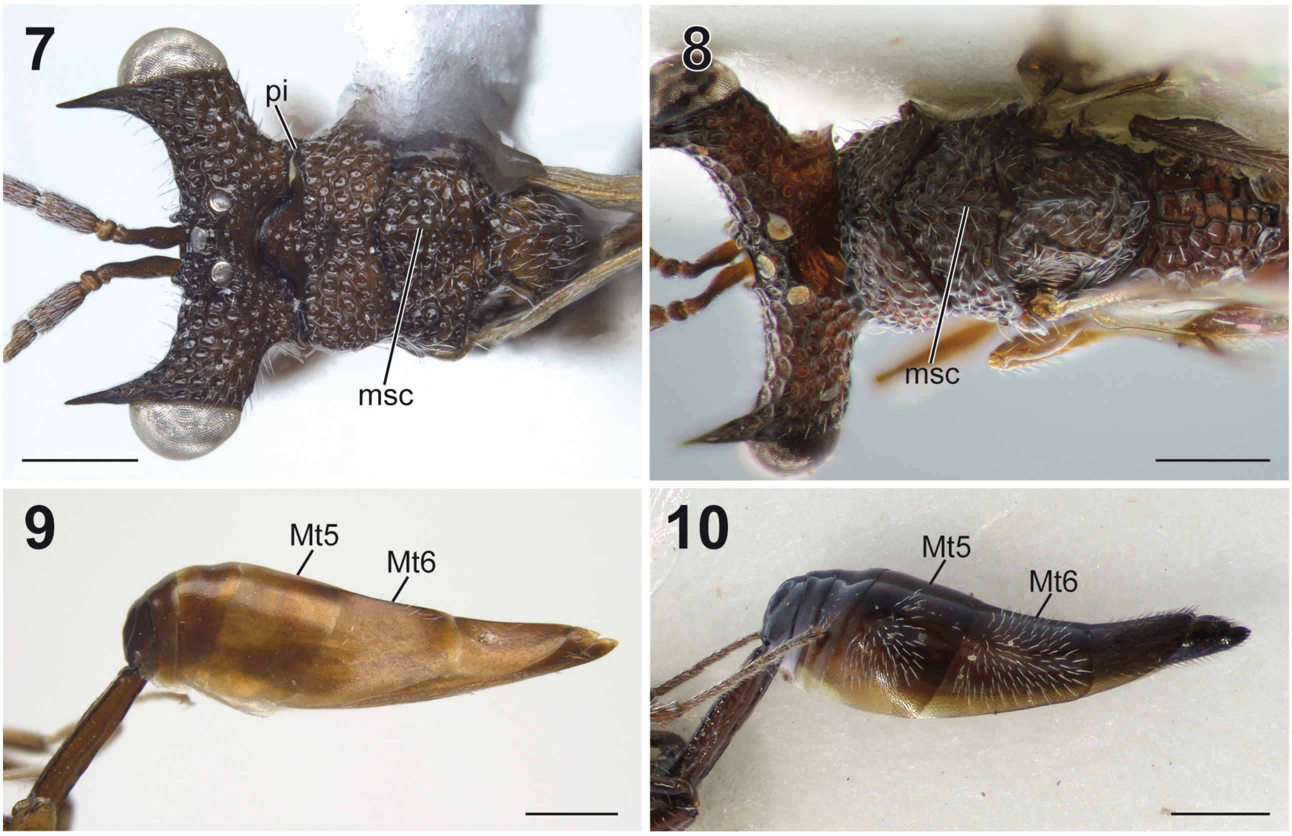
Head (Figs 1, 2, 5–7). Head punctuate, densely covered with white setae (Figs 5, 6), though less distinct, shorter and thinner, dorsally (Fig. 7). Antenna 10-segmented (Fig. 3). Length of antennal segments (in mm): scape: 0.45, pedicel: 0.06, F1 (anellus): 0.02, F2: 0.27, F3: 0.22, F4: 0.22, F5: 0.20, F6: 0.20, F7: 0.17, clava: 0.32. F2–F6 densely covered with long setae and shorter longitudinal sensilla (Fig. 3). Longitudinal sensilla arranged in multiple irregular rows (number of rows depending on length of flagellomere). Clava (Fig. 3) one-segmented, densely covered with long setae. Scrobal depression with distinct micro-reticulation.

Mesosoma (Figs 1, 2, 7). Pronotum (Fig. 7) 0.47× as long as wide; with piliferous punctures except for lateral panel of pronotum. Mesoscutum with complete and distinct notauli (Fig. 7); with a noticeable median mesoscutal carina (Figs 2, 7) that is laterally flanked by rows of piliferous foveae, remaining mesoscutum with piliferous punctures. Dorsal surface of axillae with piliferous punctures, posterior portion of axillae smooth with distinct patch of white setae. Axillulae smooth, dorsally defined by distinct carinae. Mesoscutellum expanded


**FIGURES 1–4.** *Axima sidi* Arias-Penna, Pape & Krogmann, **sp. n.** 1, habitus; 2, head and mesosoma, lateral view; 3 and 4, antenna, lateral view. Scale bars: 1, 1 mm; 2 and 3, 500 µm; 4, 100 µm. Abbreviations: cl = clava, F = flagellomere, msc = mesoscutal carina, ped = pedicel, ssc = mesoscutellar carina.




**FIGURES 5, 6.** Head. *Axima sidi* Arias-Penna, Pape & Krogmann, **sp. n.** 5, frontolateral view; 6, frontal view. Scale bars: 500 µm. Abbreviation: fp = frontal projection.




**FIGURES 7–10.** *Axima* species. 7 and 9, *Axima sidi* Arias-Penna, Pape & Krogmann, **sp. n.** 7, head and mesosoma, dorsal view; 9, metasoma, lateral view. 8 and 10, *Axima noyesi* Subba Rao (photos courtesy of N. Dale-Skey, NHM). 8, head and mesosoma dorsal view; 10, metasoma lateral view. Scale bars: 500 µm. Abbreviations: msc = mesoscutal carina, Mt = metasomal tergite, pi = pronotal invagination.

dorsally into keel-like median carina, which is continuous to the median mesoscutal carina (Figs 2, 7). Mesepisternum with distinct and broad mesofemoral depression (Fig. 2), the depression delimited anteriorly by a carina that is ventrally continuous with the epicnemial carina and consisting of two rows of impressions, an anterior row of punctures and a posterior row of foveae; mesepisternum anterior to carina with few setae. Mesepimeron (Fig. 2) glabrous, upper mesepimeron marked by deep impression, lower mesepimeron with weakly marked fovea. Ventral mesopleuron with piliferous foveae; mesofurcal pit large, situated anterior to mesotrochantinal plate;

mesodiscriminal line present. Metanotum with metascutellar arms carinate; lateral panel of metanotum consisting of row of large fovea; metascutellum carinate, reaching anterior margin but separated from posterior margin of metanotum. Hind wing tegula present, about 1/3 length of fore wing tegula. Lateral panel of metapleuron with slightly foveolate punctures and distinct white setation. Patch of white setae present on lateral metepisternum posterior to hind wing articulation (Fig. 2). Ventral metepisternum anteriorly smooth, posterior portion irregularly foveolate and greatly expanded between hind coxae. Propodeum with most piliferous punctures foveolate and much larger than on pro- and mesonotum.

Legs (Fig. 1). Fore coxa with large piliferous punctures. Mid and hind coxae setose, with microreticulation.

Wings (Fig. 1). Length of submarginal vein: 1.17 mm, marginal vein: 0.77 mm, postmarginal vein: 0.15 mm, stigmal vein: 0.09 mm.

Metasoma (Figs 1, 9). Length of metasomal tergites in dorsal view (in mm): Mt1 (petiole): 0.92, Mt2: 0.11, Mt3: 0.15, Mt4: 0.35, Mt5: 0.56, Mt6: 0.61, Mt7: 0.65, Mt8/9: 0.16. Petiole with indistinct, shallow reticulation; subrectangular in cross section, with four strong carinae delineating each of the dorso- and ventrolateral margins; dorsal surface with median carina along anterior ¾; lateral surface with additional complete length carina. Post-petiolar metasoma with shallow microreticulation; tergites bare except Mt6 with few isolated setae, Mt7 with patch of setae posterior to spiracles and Mt8/9 setose (Fig. 9). Length of exposed part of ovipositor in dorsal view: 0.10 mm.

Male. Unknown.

**Distribution.** Colombia: Amazonas.

**Etymology.** This species is named after Sid, the lazy but big-hearted ground sloth that features in the computer-animated comedy adventure series *Ice Age*. The name is based on facial resemblance between these two, which is mainly caused by shared bulbous eyes, and the characteristic anteroventral orientation of accompanying structures (hairs in the ground sloth/cuticular frontal projections in the new species).

**Host.** Unknown.

**Comment.** No anellus was described in the two other known species of the *A. noyesi* species group. The anellus is present in *A. noyesi* and can even be traced in the original drawing of the holotype (Subba Rao 1978, figs 17, 18). A re-examination of the slide-mounted antenna of the holotype of *A. diabolus* revealed the presence of a minute, almost linear anellus (Gibson, pers. comm.).

## Discussion

Despite their large body size and their morphological distinctiveness, stalk-eyed wasps have been rarely collected. The "Insect Survey of a Megadiverse Country, Phase I & II: Colombia" collected 450 samples in Amacayacu National Park during four years, which included 297 samples from Malaise traps and sweeping (Arias-Penna 2007). Tens of thousands of Hymenoptera were sorted from this material, partly by the senior author, but no stalk-eyed *Axima* were recovered. The present female, and the unique female holotypes of the other two described species, were collected by sweep netting. Because males of stalked-eyed wasp species are unknown, it remains to be seen whether the head modification is present in both sexes. The degree of sexual dimorphism in Eurytominae usually is moderate, with males differing from females principally in antennal morphology (Gates *et al.* 2006). In "normal-eyed" *Axima* species sexual dimorphism is restricted to antennal morphology, males being characterized by pedunculate funicular segments with longer setae. Males of *A. zabriskiei* share the short frontal projections on the head with females, which indicates a morphological adaption to a lifestyle or behavioural trait that is not related to gender. *Axima zabriskiei* has been reared from *Ceratina dupla* Say and *C. calcarata* Robertson, carpenter bees that nest in the soft pith of plants such as elder (*Sambucus* spp., Adoxaceae), sumac (*Rhus* spp., Anacardiaceae), blackberry (*Rubus* spp., Rosaceae), raspberry (*Rubus strigosus*, Rosaceae) (Rau 1928) and teasel (*Dipsacus fullonum*, Dipsacaceae) (Vickruck *et al.* 2010). The sharp and acutely pointed frontal projections on the head (Figs 5, 6) might facilitate the emergence through the surrounding soft plant tissue. Some groups of parasitoids that need to emerge from hosts enclosed in wood have a completely different adaptation that might be called a "head butting device". Chalcidoid parasitoids of wood-boring insects, such as Pteromalidae: Cleonyminae (Gibson 2003, figs 388, 389, 449) or Pteromalidae: Leptofoeninae (Krogmann & Burks 2009, fig. 2B) have rows of rough spines on the head. Similar spines are found in other parasitoid wasp groups with hosts in wood, such as Stephanidae, Orussidae, Diapriidae (*Psilus* spp.) and Braconidae (Quicke 1997).

Species of *Dirhinus* Dalman (Chalcididae) are parasitoids of muscoid flies such as *Musca domestica* Linnaeus, the common house fly (Alahmed 1999, Beaver 1986, Bouček & Narendran 1981). Their head bears a pair of projections because the frons is dramatically produced on either side of a deep excavation in which the antennae reside. In some species of *Dirhinus*, e.g., *D. himalayanus* Westwood, the broad projections may be used by the adult female to shovel through a sandy substrate in search of host puparia (Bouček & Narendran 1981). In all these examples the head modifications are present in both sexes.

In the stalk-eyed wasp species *A. diabolus*, *A. noyesi* and *A. sidi*, females have frontal projections that are even more pronounced than in their "normal-eyed" congeners. The head morphology of stalk-eyed wasps might be interpreted as a further development of an already existing "head butting device". Such a function could be further supported by the fact that the head of *Axima* species can be locked by pronotal invaginations (Fig. 7). After the head is locked, more force can be exerted through the anteroventrally oriented frontal projections for butting or thrusting forward through plant tissue. However, the difference to the head modification in the above-mentioned parasitoids of wood boring hosts is that these emerge upward (not forward) using the dorsally oriented projections to leave the host's burrow. In other insect groups the development of stalked eyes is never accompanied by sclerotized lateral projections, which would seem to exclude a similar "tool-function". In hypercephalic Diptera, stalked eyes have been discussed with respect to enhanced vision for binocularity (Grimaldi & Fenster 1989), but sexual selection seems to play an important role (Zimmer 2008).

Until the host biology of stalk-eyed wasps is revealed, the possible function of the stalks as "head butting devices" for emergence from the host or the host habitat will remain uncertain. However, the presence of frontal projections in both sexes of other *Axima* species could support the hypothesis of eye stalks as a further adaption for escape from hosts enclosed in soft pith of plant stems.

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