

SUPPLEMENTAL INFORMATION

Supplemental Information includes two tables, experimental procedures, and references and can be found with this article online at <https://doi.org/10.1016/j.cub.2018.06.031>.

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AUTHOR CONTRIBUTIONS

M.R. conceived and designed the study, M.V. and J.Ž. collected field data, M.P. performed histological analysis, and M.V. and M.R. drafted the manuscript.

REFERENCES

- Williams, D.D. (2007). *The Biology of Temporary Waters*. (Oxford: Oxford University Press).
- Cellerino, A., Valenzano, D.R., and Reichard, M. (2016). From the bush to the bench: the annual *Nothobranchius* fishes as a new model system in biology. *Biol. Rev.* 91, 511–533.
- Hu, C.K., and Brunet, A. (2018). The African turquoise killifish: A research organism to study vertebrate aging and diapause. *Aging Cell* 17, e12757.
- Blažek, R., Polačik, M., and Reichard, M. (2013). Rapid growth, early maturation and short generation time in African annual fishes. *Evodevo*. 4, 24.
- Blažek, R., Polačik, M., Kačer, P., Cellerino, A., Řežucha, R., Methling, C., Tomášek, O., Syslová, K., Terzibasí Tozzini, E., Albrecht, T., et al. (2017). Repeated intraspecific divergence in lifespan and ageing of African annual fishes along an aridity gradient. *Evolution* 71, 386–402.
- Polačik, M., Blažek, R., and Reichard, M. (2016). Laboratory breeding of the short-lived annual killifish *Nothobranchius furzeri*. *Nat. Protoc.* 11, 1396–1413.
- Vrtilek, M., Žák, J., Polačik, M., Blažek, R., and Reichard, M. (2018). Longitudinal demographic study of wild populations of African annual killifish. *Sci. Rep.* 8, e4774.
- Furness, A.I., Reznick, D.N., Springer, M.S., and Meredith, R.W. (2015). Convergent evolution of alternative developmental trajectories associated with diapause in African and South American killifish. *Proc. Biol. Sci.* 282, 20142189.
- Karsten, K.B., Andriamandimbarisoa, L.N., Fox, S.F., and Raxworthy, C.J. (2008). A unique life history among tetrapods: An annual chameleon living mostly as an egg. *Proc. Natl. Acad. Sci. USA* 105, 8980–8984.

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The cephalo-thoracic apparatus of *Caputoraptor elegans* may have been used to squeeze prey

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Alienoptera is an insect order recently described from mid-Cretaceous amber [1] and is phylogenetically nested in the Dictyoptera lineage. Alienoptera currently comprises three species: *Alienopterus brachyelytrus* [1], *Alienopterella stigmatica* [2] and *Caputoraptor elegans* [3]. The most interesting is *Caputoraptor elegans*, which was recently described in *Current Biology* by Bai and colleagues [3] and which has an unusual cephalo-thoracic device formed by wing-like extensions of the genae and the corresponding edges of the pronotum. Bai and colleagues [3] suggested that the cephalo-thoracic apparatus may have been used to hold the female and male together during copulation. According to this possible function, the cephalo-thoracic apparatus of the female would fit together with the spread forewings of the male while the female was on the back of the male during copulation. This function was proposed based on examination of females and nymphs, and the authors stated that it could be falsified if a male with a similar apparatus were discovered. After examining a male nymph of this species (Figure 1), I here suggest that the cephalo-thoracic apparatus was not used for copulation but was instead used for predation and feeding.

The hypothesis that females use the cephalo-thoracic apparatus to hold onto males during copulation is improbable for two reasons. First, if the apparatus was used only for coupling, it would not be developed (or fully developed) in nymphs where it would not fulfil its purpose. Second, a character that is related to coupling and that occurs in only one of the sexes is almost always subject to sexual selection. Such selection, however, usually leads to

sex-specific features in the sex with less investment in offspring, *i.e.*, in the sex that produces microgametes, and these are the males [4,5]. Because males are exposed to more intense sexual selection than females, conspicuous secondary sexual characters usually evolve in males rather than in females [6]. Although exceptions exist in insects [7], they are rare and related to cases in which male investment in offspring involves more than sperm donation, as is the case in Heteroptera: Belostomatidae [8]. Such a case, however, is unknown in dictyopteran insects [9,10].

As indicated above, the hypothesis about the use of the cephalo-thoracic device by the female seems unlikely due to the finding of a male nymph (Supplemental Information) with the fully developed apparatus. The studied nymph has nine visible abdominal coxosternites (Supplemental Information), and it is therefore an immature male. Bai and colleagues [3] also suggested that the cephalo-thoracic device may have been used for capturing prey or for defence.

A detailed study of the morphology of the cephalo-thoracic apparatus in the studied nymph (Figure 1; Supplemental Information) has revealed new findings that provides insight into its probable function. The area between the posterior part of the head (gula) and the anterior part of the pro- and mesothorax forms a cavity (Figure 1A). A sharp ridge surrounds the cavity, except in the area of the mouth and of the gap for the forelegs. The thoracic part of the ridge consists of projections of the pro- and mesonotum. The pronotal projections have a straight serrate distal part and a non-serrate proximal part, and these parts curve towards each other. A narrow, sharp extension of the mesonotum abuts the pronotal part and borders the gap for the forelegs.

If the cephalo-thoracic device is closed, the edge of the pronotal ridge is inserted beneath the edge of the wing-like extensions of the genae, and the non-serrate proximal part of the pronotal ridge fits into the narrow groove in the gula under a part of the gena and subgena. The short mesonotal ridge probably attaches to the distal part of the maxillae (stipes) in the closed stage. The closed cephalo-thoracic device remains opened only in the space formed partly



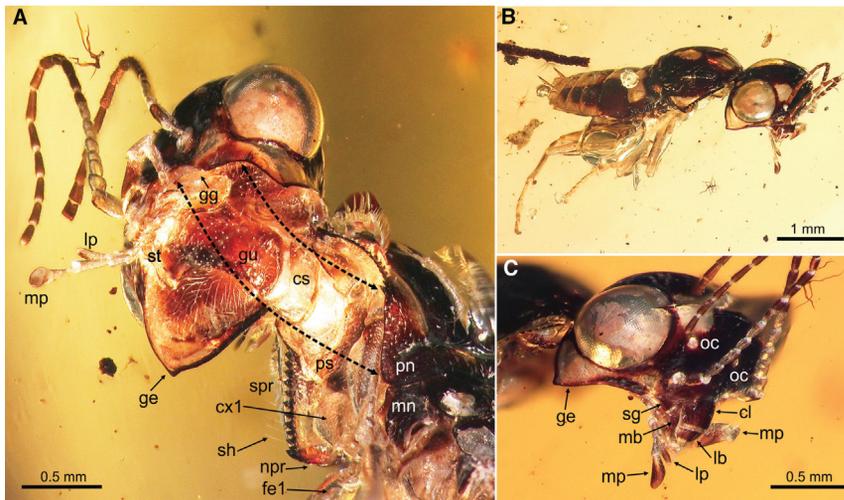


Figure 1. A male nymph of *Caputoraptor elegans*.

(A) Latero-ventral view of head and thorax. (B) Lateral view of the entire body. (C) Antero-lateral view of head. Arrows connected by dashed lines in (A) indicate the complementary structures of the head and the thoracic parts of the cephalo-thoracic apparatus. Abbreviations: cl – clypeus, cs – cervical sclerite, cx1 – procoxa, fe1 – profemur, ge – genae, gg – gula groove, gu – gula, lb – labrum, lp – labial palpus, mb – mandibula, mp – maxillary palpus, mn – mesonotum, npr – non-serrate part of pronotal projection, oc – ocellus, pn – pronotum, ps – prosternum, sg – subgena, sh – sensory hairs, spr – serrate part of pronotal projection, st – stipes.

by the mouth and partly by the groove between the distal parts of the procoxae. The lateral sides of the cephalo-thoracic cavity taper forward to the mouth. The mandibles are very small for a predator, and the whole mouthpart protrudes from the head capsule and triangularly tapers antero-ventrally (Figure 1C). The procoxae are enlarged, with a swollen central part (Figure 1A), and are distally tapered to the hole bordered by the short ridges of the mesonotum. The inner parts of the procoxae have a roughened surface that might serve to entrap liquid food (Supplemental Information). Given the arrangement of the legs, *Caputoraptor elegans* was probably able to climb even when the cephalo-thoracic device was closed and even if the device was grasping prey.

Based on the morphological observations detailed in the previous two paragraphs, I propose that the cephalo-thoracic apparatus was used to catch and hold prey, and was then used to squeeze the prey and enable the predator to feed on the body fluids released from injuries caused by the toothed projections of the pronotum. The prey fluids (hemolymph, fat body) presumably flowed from the cavity of the cephalo-thoracic ‘press’ device to the mouth. The functional components

of this press device were the gula, prosternum, and probably also the procoxae of the forelegs. The procoxae with expanded middle parts fit well into the lateral depressions of the gula, and the groove between both procoxae could have been used to direct the liquid food to the predator’s mouth. Movements of the coxae could also increase the pressure applied by the cephalo-thoracic apparatus and thus accelerate and regulate the flow of fluid. The sensory hairs on the pronotal ridge of the apparatus (Figure 1A), described also by Bai and colleagues [3], may have functioned as tactile mechanoreceptors triggering its closing. In summary, I suggest that *Caputoraptor elegans* was a predator that fed on the body fluids of its prey. It obtained access to those body fluids by injuring the prey (with the toothed projections of the pronotum) and then by using the cephalo-thoracic apparatus to squeeze the prey so that the fluids were forced out of the prey’s body. The apparatus may have also functioned in the defense against predators.

I agree with Bai and colleagues [3] that *Caputoraptor elegans* may have been a predator that specialized on soft-bodied insects. Because the cephalo-thoracic device was certainly not usable

in cramped areas such as under the soil surface or under bark, the prey were probably slow-moving arthropods that lived aboveground on herbs, shrubs, or trees. Given its large eyes and aposematic coloration (Figure 1B), *Caputoraptor elegans* was probably active during the day.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and one figure can be found with this article online at <https://doi.org/10.1016/j.cub.2018.06.046>.

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REFERENCES

- Bai, M., Beutel, R.G., Klass, K.D., Zhang, W., Yang, X., and Wipfler, B. (2016). Alienoptera – a new insect order in the roach-mantodean twilight zone. *Gondwana Res.* 39, 317–326.
- Kočárek, P. (2018). *Alienopterella stigmatica* gen. et sp. nov.: the second known species and specimen of Alienoptera extends knowledge about this Cretaceous order (Insecta: Polyneoptera). *J. Sys. Palaeontol.* <https://doi.org/10.1080/14772019.2018.1440440>.
- Bai, M., Beutel, R.G., Zhang, W., Wang, S., Hörnig, M., Gröhn, C., Yan, E., Yang, X., and Wipfler, B. (2018). A new Cretaceous insect with a unique cephalo-thoracic scissor device. *Curr. Biol.* 28, 438–443.
- Trivers, R. (1972). *Parental Investment and Sexual Selection* (Cambridge, MA: Biological Laboratories, Harvard University).
- Møller, A.P., and Thornhill, R. (1998). Male parental care, differential parental investment by females and sexual selection. *Anim. Behav.* 55, 1507–1515.
- Panhuis, T.M., Butlin, R., Zuk, M., and Tregenza, T. (2001). Sexual selection and speciation. *Trends Ecol. Evol.* 16, 364–371.
- Parker, G.A., and Simmons, L.W. (1996). Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proc. R. Soc. Lond. B* 263, 315–321.
- Smith, R.L. (1979). Paternity assurance and altered roles in the mating behaviour of a giant water bug, *Abedus herberti* (Heteroptera: Belostomatidae). *Anim. Behav.* 27, 716–725.
- Bell, W.J., Roth, L.M., and Nalepa, C.A. (2007). *Cockroaches: Ecology, Behavior, and Natural History* (Baltimore: JHU Press).
- Wieland, F. (2013). The phylogenetic system of Mantodea (Insecta: Dictyoptera). *Spec. Phyl. Evol.* 3, 3–222.

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