As the Worm Turns: Speciation and the Apple Maggot Fly

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Hawthorn trees grow throughout North America and they produce a small fruit which is eaten by a small fly larva. In 1864, apple growers discovered an unknown maggot had started feeding on apples. Through the years, hawthorn and apple maggot flies have progressively become more distinct.

Below I present evidence taken from the original scientific literature for you to consider and evaluate. From what may be incomplete and ambiguous data, I hope you will be able to answer what appear to be two simple questions:

1. Do hawthorn maggot flies and apple maggot flies belong to the same species?

2. If not, and if apple maggot flies belong to their own species, what would be a biologically reasonable scenario for how the speciation occurred?

Facts about Hawthorn and Apple Maggot Flies (*Rhagoletis pomonella*)

The Organisms

The apple maggot fly (*Rhagoletis pomonella*, Walsh) is native to eastern North America. It originally bred in the large fruits of hawthorn trees (Reissig, 1991).

Figure 1: Apple maggot flies (male—left, female—right)

Apple maggot flies are about 5 mm long. The tip of a female's abdomen is more narrowly pointed than a male's.

Hawthorn and apple maggot flies are assigned to the same taxonomic species (*Rhagoletis pomonella*) (Bush, 1966; Bush, 1969; Bush, 1975: cited in Berlocher and Feder, 2002).

- Hawthorn maggot flies and apple maggot flies are physically indistinguishable.
- There is no geographic isolation or physical separation between adult maggot flies.
- As host-races of the same species, these flies are not typically given different common names.

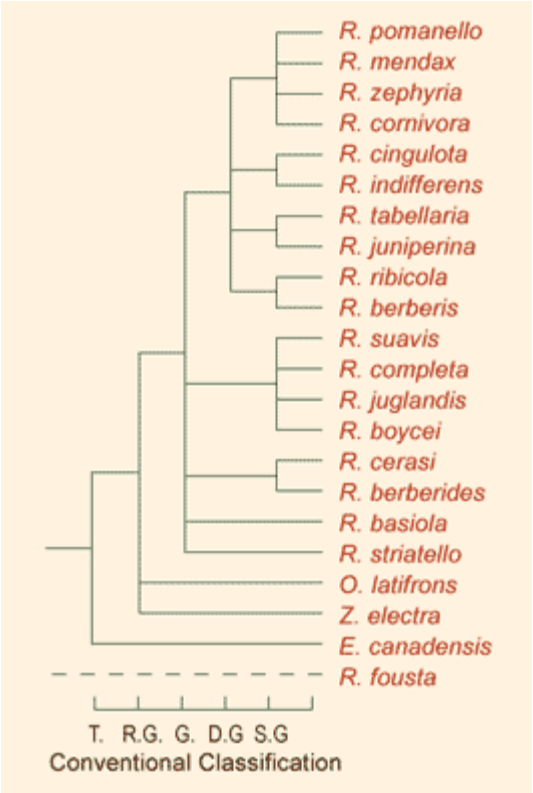

Figure 2: Taxonomic Tree of *Rhagoletis* (adapted from Berlocher and Bush, 1982)

R. pomonella belongs to a set of four fly species that cannot be physically distinguished.

Figure 2 displays the conventional classification of *Rhagoletis*. The abbreviated categories are: tribe (*T.*), closely related genera (*R.G.*), genus (*G.*), derived species groups (*D.G.*), and species group (*S.G.*). The classification bar at the bottom of the figure arranges the nodes of divergence from the most inclusive taxonomic category (the tribe, *T*) to groups of closely related species (species groups, *SG*).

Maggot Fly Reproduction

- The female fly lays fertilized eggs into the fruit (Reissig, 1991).
- Maggots (larvae) emerge from the egg, eat and grow, and puparite where the last larval skin is retained and hardened to form the protective covering for metamorphosis (Reissig, 1991).
- Pupariating individuals develop into adult flies, emerge and reproduce (Reissig, 1991).

Figure 3: Apple spoiled by apple maggot larvae.

Facts about Hawthorn and Apple Plants

Both the hawthorn and the apple are woody plants belonging to the same taxonomic family (the Rose Family) (Newcomb, 1977).

Figures 4a and 4b: Photo and diagram of *Crataegus marshallii*.

- Hawthorns are native to North America.
- Hawthorns are a large and complex group of trees and shrubs with over 50 species native to North America (North-eastern and North-central).
- Hawthorns belong to the plant genus *Crataegus*.
- Most hawthorn species are identified by fruits that differ in size—for example, *C. marshalli* has a fruit that is 4.9 mm in diameter, while *C. pedicellata* has a fruit that is nearly four times larger (19.5 mm).

The apple is the most widely grown fruit in North America (Seelig and Hirsh, 1978).

- Apples belong to the plant genus *Malus*. The taxonomic name *Malus domesticus* is preferred for the large-fruited, edible apple.
- Early European colonists brought both seeds and grafted apple trees to North America. Records of grafting desirable apple varieties onto wild rootstocks date back to 1647 in Virginia.

Figure 5: Empire red apples.

Figure 6 below is a general representation of the timing of fly emergence (solid and dashed lines) and fruit ripening (colored filled-in curves). Adult flies emerge from the puparium to reproduce before fruits are mature (Reissig, 1991). Apple fruits ripen approximately 1 month earlier than hawthorn fruits, *but there is overlap* at the end of the apple fruiting season and the beginning of the hawthorn fruiting season (Feder and Filchak, 1999; Feder *et al.*, 1994; Filchak and Feder, 1999; Smith, 1988: cited in Berlocher and Feder, 2002). The female fly then lays fertilized eggs into the ripe fruit (Reissig, 1991). Maggots (larvae) hatch from the egg, eat fruit, grow, and pupate (Reissig, 1991).

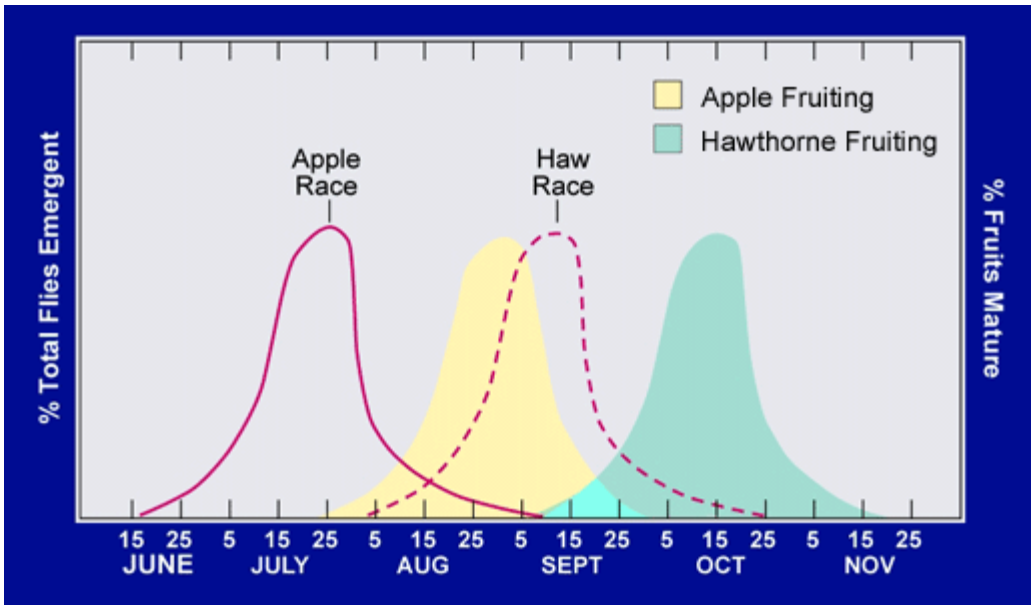

Figure 6: Emergence of *Rhagoletis pomonella* (adapted from Bush, 1969)

In Figure 6, the taxonomic term "race" is used to identify the maggot flies that reproduce on apples or the maggot flies that reproduce on hawthorns.

In 1864 maggot flies were first noted to infest apples grown in New York's Hudson River Valley (Bush, 1969).

- Maggot flies ultimately became a major fruit pest in the northeastern United States and Canada (Reissig, 1991).
- Thorough control of the maggot flies is needed to produce the highest quality and most marketable fruits (Reissig, 1991).

Figure 7: Blemishes indicate burrowing larvae.

Fruit Characteristics

Apples are bigger fruits than hawthorns.

- The typical commercial apple fruit has a diameter of 2.75 inches (70 mm).
- The typical wild hawthorn fruit has a diameter of 0.5 inches (12.6 mm).

The larger fruits of apple trees provide 5.5 times more depth (based on diameter) to developing maggots than do hawthorn fruits.

- Parasitoid wasps lay eggs into the maggot's body, with the wasp larvae ultimately killing the maggot.
- Apple maggots are better able to escape parasitoid wasps by burrowing deeper into the fruit than the wasp can penetrate with its egg-layer (ovipositor) (Feder, 1995: cited in Berlocher and Feder, 2002).
- Apple maggots bear 70% fewer parasitoid wasp eggs than do hawthorn maggots (Feder, 1995: cited in Berlocher and Feder, 2002).

The larger fruits of apple trees provide 220 times more food (based on volume) to the growing and developing maggot than the smaller fruits of hawthorns.

- Apple maggot flies lay more eggs per fruit than do hawthorn maggot flies.
- Though the bigger apple provides more food (quantity), it does not provide better food (quality) to the growing maggot (Reissig and Smith, 1978: cited in Berlocher and Feder, 2002).
- The nutritional quality of hawthorn fruit is indicated by the better survival of both types of maggots in hawthorn fruits; 52% of maggot fly eggs survived in hawthorn fruits and 27% of maggot fly eggs survived in apple fruits (Prokopy *et al.*, 1988 cited in p. 329 Freeman and Herron, 1998).
- Caterpillars and weevils may also feed on the larger apple, reducing the quantity of food available to apple maggots.

Evolutionary Outcomes in Apple Maggot Flies

- Fidelity to fruit type acts as a strong barrier to gene flow between the two types of maggot flies.
- There is only a 4 to 6% hybridization rate between hawthorn maggot flies and apple maggot flies (Feder, 1998; Feder *et al.*, 1994: cited in Berlocher and Feder, 2002).
- Hawthorn maggot flies strongly prefer to mate on and lay fertilized eggs into hawthorns.
- Apple maggot flies strongly prefer to mate on and lay fertilized eggs into apples.
- Hawthorn and apple maggot flies are genetically distinguishable (have recognizable genetic profiles) (Feder, 1998; Feder *et al.*, 1988; Feder *et al.*, 1997; McPheron *et al.*, 1988: cited in Berlocher and Feder, 2002)

Questions

In your groups, address the following and list the evidence used to make your decisions.

1. What species concept should be used in this case?
2. Are apple maggot flies distinct as a species from hawthorn maggot flies?
3. Propose a biologically reasonable scenario that explains how apple maggot flies evolved.
4. How did you weigh the different pieces of evidence to reach a conclusion to questions (2) and (3)? What evidence was most important, what was least important, etc.?
5. What further information would you need to increase your confidence in the conclusions you reached?

References

- Berlocher, S.H. and G.L. Bush. 1982. An electrophoretic analysis of *Rhagoletis* (Diptera: Tephritidae) phylogeny. *Systematic Zoology* 31:136-155.
- Berlocher, S.H. and J.L. Feder. 2002. Sympatric speciation in phytophagous insects: moving beyond controversy? *Annual Review of Entomology* 47:773-815.
- Bush, G.L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). *Evolution* 23:237-251.
- Freeman, S. and J.C. Herron. 1998. *Evolutionary Analysis*. Upper Saddle River, NJ: Prentice-Hall.
- Freeman, S. and J.C. Herron. 2001. *Evolutionary Analysis*, 2nd edition. Upper Saddle River, NJ: Prentice-Hall.
- Newcomb, L. 1977. *Newcomb's Wildflower Guide (NE and NC North America)*. Boston: Little Brown and Co.
- Prokopy, R.J., S.R. Diehl and S.S. Cooley. 1988. Behavioral evidence for host races in *Rhagoletis pomonella* flies. *Oecologia* 76:138-147.
- Reissig, W.H. 1991. Insect Identification Sheet No. 7: Apple Maggot, *Rhagoletis pomonella* (Walsh). Cornell University and the New York State IPM Program.
- Seelig, R.A. and D. Hirsh. 1978. March - Fruit and vegetable pointers: Apples. United States Fresh Fruit and Vegetable Association. Washington, DC.

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