Name: ______________________________ SSN (last 4 digits): ____________

UNIVERSITY OF HOUSTON

FALL SEMESTER, 2004

BIOLOGY

BIOL4397 — Evolution of Development

NOTE: The maximum score is **100 points**. Answer all true/false or multiple choice questions by ticking boxes; other kinds of answers will be ignored. An incorrect, non-blank answer to a true/false question will incur a deduction of 25% of its score. Time allowed: **50 minutes**.

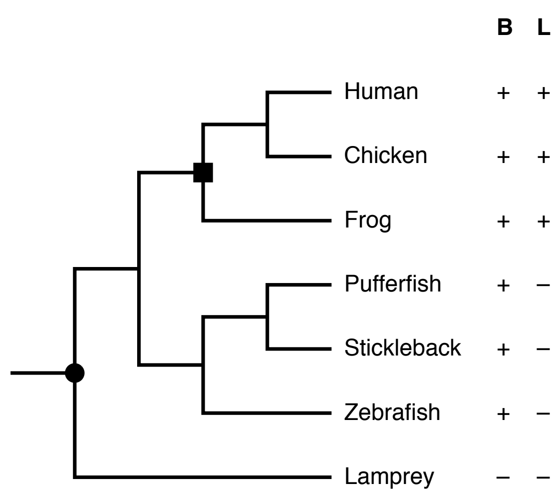

Figure 1: Phylogenetic relationships among 7 species of chordates: african clawed frog (*Xenopus laevis*), chicken (*Gallus gallus*), human (*Homo sapiens*), lamprey (*Petromyzon marinus*), pufferfish (*Takifugu rubripes*), three-spine stickleback (*Gasterosteus aculeatus*) and zebrafish (*Danio rerio*). The circle and square represent hypothetical ancestors. +/− signs indicate presence/absence of bone (B) and paired limbs (L).

1. Evaluate the following statements concerning the phylogeny in Fig. 1: **[2 points each]**

(a) The species possessing bone (B+) form a monophyletic group. True [×] False [ ]

(b) The presence of bone (B+) is a derived homology in chicken, frog and human. True [ ] False [×]

(c) The presence of bone (B+) is a homoplasy in pufferfish and stickleback. True [ ] False [×]

(d) The species possessing paired limbs (L+) form a paraphyletic group. True [ ] False [×]

(e) The absence of paired limbs (L−) is an ancestral homology in pufferfish, stickleback and zebrafish. True [×] False [ ]

2. Imagine the most parsimonious scenarios for the evolution of bone and paired limbs using only the data in Fig. 1. Evaluate the following statements: **[2 points each]**

(a) The limbs of frog and human are the result of convergent evolution. True [ ] False [×]

(b) The earliest ancestor that possessed bone is represented by a circle. True [ ] False [×]

(c) The earliest ancestor that possessed paired limbs is represented by a square. True [×] False [ ]

(d) The absence of limbs in pufferfish, stickleback and zebrafish denotes a selective constraint on limb development in these species. True [ ] False [×]

(e) The presence of bone leads to higher fitness. True [ ] False [×]

3. *Sox8* and *Sox9* are members of the Sox family of transcription factors (Fig. 2). Evaluate the following statements about vertebrate *Sox8* and *Sox9* genes: **[2 points each]**

(a) Human *Sox9* and zebrafish *Sox9a* are orthologs. True [×] False [ ]

(b) Chicken *Sox9* and pufferfish *Sox9b* are paralogs. True [ ] False [×]

(c) Human *Sox8* and *Sox9* are orthologs. True [ ] False [×]

(d) Zebrafish *Sox9a* and pufferfish *Sox9b* are paralogs. True [×] False [ ]

(e) Human *Sox9* is more similar to zebrafish *Sox9a* than to zebrafish *Sox9b*. True [ ] False [×]

CONTINUED

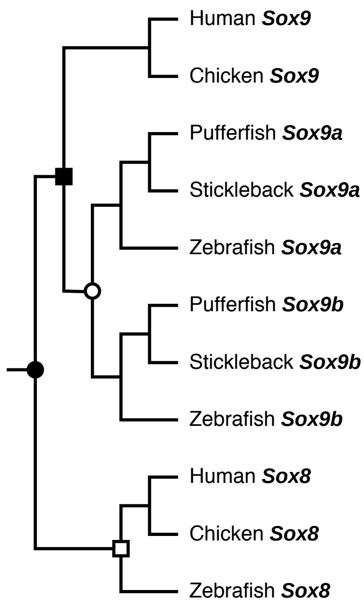

Figure 2: Gene tree for *Sox8* and *Sox9* genes in a subset of the species represented in Fig. 1. Circles and squares represent hypothetical ancestral genes.

4. Imagine the most parsimonious scenario for the evolution of vertebrate *Sox8* and *Sox9* genes using only the data in Figs 1 and 2. What is the lowest number of ancestral Sox gene duplications required to explain the observed pattern? (Choose one.) **[5 points]**

(a) One gene duplication of the gene represented by a closed circle. [ ]

(b) Two successive gene duplications of the gene represented by a closed circle. [ ]

(c) Two gene duplications: one by the gene represented by a closed circle, and one by the gene represented by an open circle. [×]

(d) Three gene duplications: one by the gene represented by a closed circle, and two by the gene represented by a closed square. [ ]

(e) Four gene duplications: one by each gene represented by a symbol. [ ]

5. According to the "classical" model for the preservation of gene duplicates, the probability of preservation of a *Sox* gene after gene duplication is expected to be (choose one): **[5 points]**

(a) High because selection tends to prevent the degeneration of any gene. [ ]

(b) Low because deleterious mutations occur more frequently than beneficial ones, and the degeneration of one duplicate copy will be nearly neutral due to redundancy. [×]

(c) High because mutations tend to create new and essential protein functions for one of the duplicate copies. [ ]

(d) Low because most mutations are neutral. [ ]

6. According to the DDC model for the preservation of gene duplicates, the probability of preservation of a *Sox* gene after gene duplication is expected to be (choose one): **[5 points]**

(a) The same as under the "classical" model, provided that both the population size and the mutation rate are assumed to be the same under both models. [ ]

(b) Higher than under the "classical" model, because degenerative regulatory mutations often lead to the partitioning of ancestral subfunctions among descendant gene duplicates. [×]

(c) Higher than under the "classical" model, because the DDC model assumes a lower mutation rate and a more complex type of gene regulation than the "classical" model. [ ]

(d) Lower than under the "classical" model, because genes with complex regulatory regions are more likely to degenerate under mutational pressure. [ ]

7. In zebrafish and stickleback embryos, *Sox9a* is expressed in the mandibular and hyoid arches, whereas *Sox9b* is expressed in the trunk neural crest. What is the expected expression pattern of *Sox9* in human and chicken, according to the DDC model? Explain. **[10 points]**

The DDC model predicts that the ancestor represented by a filled square (Fig. 2) would have expressed Sox9 *in both the MHA and the TNC, and that the modern expression patterns of* Sox9a *and* Sox9b *in fish result from the partitioning of ancestral subfunctions among the duplicates. The most parsimonious scenario is that the ancestral* Sox9 *expression pattern has been retained in the embryos of both chicken and human. Therefore, the DDC model predicts that* Sox9 *should be expressed in both the MHA and the TNC in both human and chicken embryos.*

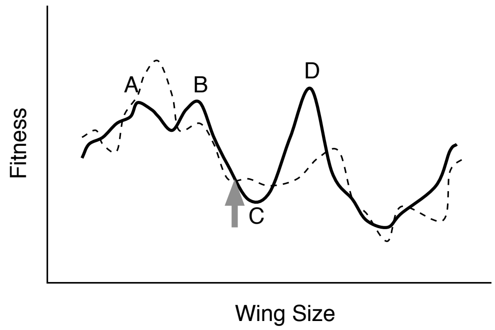

Figure 3: Hypothetical fitness landscapes for wing size in *Drosophila*.

8. Imagine that a population of flies is subject to the fitness landscape represented by the bold line (Fig. 3). The arrow indicates the current mean wing size in the population. Assuming that the heritability of wing size is high, evaluate the following statements: **[2 points each]**

(a) The mean wing size of the population will move towards peak B. True [×] False [ ]

(b) The mean wing size of the population is less likely to move towards peak A than towards peak D because the latter is the global optimum. True [ ] False [×]

(c) If the population is small, the mean wing size of the population might move towards valley C due to genetic drift. True [×] False [ ]

(d) A change in the environment could change the fitness lanscape to that represented by a dashed line. True [×] False [ ]

(e) A mutational constraint could change the fitness lanscape to that represented by a dashed line. True [ ] False [×]

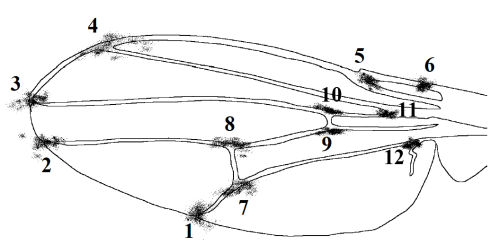

Figure 4: Diagram of a *Drosophila* wing. Clouds of points show the size-adjusted positions of wing vein intersections for 2774 flies from 23 species of the family Drosophilidae.

9. Drosophilids show a highly conserved type of flight: slow, hovering, reminiscent of a "cargo-helicopter". In addition, while the wings of drosophilid flies of different species differ considerably in size, the size-adjusted positions of wing vein intersections are remarkably conserved (Fig. 4).

(a) Are these comparative observations consistent with the presence of a developmental constraint on the positions of wing vein intersections in drosophilids? Explain. **[10 points]**

Yes, this pattern is consistent with a developmental constraint. Lack of variation among closely related species in any trait is evidence for the existence of a constraint on that trait, but this constraint is not necessarily caused by a property of the developmental system (developmental constraint). For example, stabilizing selection on flight ability might select against deviations from the conserved pattern of wing venation (selective constraint).

(b) How would you test whether the lack of interspecific variation in the positions of wing vein intersections of drosophilids is caused by lack of genetic variation. **[15 points]**

Lack of genetic variation for wing vein positions could be tested using a variety of artificial selection experiments in Drosophila *species. For example, we could try to select for changes in the position of the vein intersection 8 relative to intersections 2 and 9. If it were possible to produce wings with patterns deviating strongly from the conserved pattern, the hypothesis of lack of genetic variation would be falsified. Based on Weber's work (discussed in lecture 8), such an outcome would be quite likely. Other approaches might also be considered, such as, mutation accumulation and mutagenesis.*

(c) Speculate about how generative and selective constraints might affect the positions of wing vein intersections in drosophilids. **[10 points]**

A generative constraint would be the inability of drosophilids to generate variant morphologies during development. A selective constraint would occur if variant wing vein morphologies could be generated during development but were selected against.