Bilateral symmetry is one of the most widespread morphological characters in animals. Yet, even animals with a well-defined bilaterally symmetrical body plan (e.g. most Bilaterians) are generally *not strictly* symmetrical, since many structures such as vertebrate internal organs are obviously asymmetrical or even unilateral (Babcock, 2005; Palmer, 1996; Van Valen, 1962). The breaking of symmetry can however take many other forms, sometimes less evident, with different biological implications (Klingenberg, 2022; Palmer, 1994; Van Valen, 1962).

The differences between left and right sides can be subtle, requiring precise quantitative measurements to be detected, or conspicuous, i.e. visible directly upon observation. Among subtle asymmetry types, fluctuating asymmetry is arguably the most studied, due to being an assumed proxy for developmental instability, relating to intrinsic or extrinsic stresses on organisms (Benítez et al., 2020; Graham et al., 1993; Klingenberg, 2022; Møller, 1990; Palmer, 1994; Savriama et al., 2016; Van Valen, 1962). When studying fluctuating asymmetry, it is assumed that symmetry is the norm and the target phenotype to achieve (Hansen et al., 2006), and that stresses will lead to small random left-right differences, the distribution of which should be normal and centered on 0 (i.e. on perfect symmetry) at the population level (Palmer, 1994). Subtle asymmetry types also include directional asymmetry and antisymmetry, in which a symmetrical phenotype is *not* the norm, with the left-right differences being of consistent direction in the case of directional asymmetry, leading to a normal distribution *not* centered on 0, or of random direction in antisymmetry, leading to a platykurtic or bimodal distribution of differences. Directional asymmetry and antisymmetry are also found, and generally characteristic for conspicuous asymmetries (Palmer, 2004). In this case again, a symmetric phenotype is not the norm, and the target phenotype is visibly different between left and right sides.

Because directional asymmetry and antisymmetry entail systematic differences between sides, they are generally considered to be inherited, and possibly to be adaptive. The latter point is however dependent on whether subtle or conspicuous asymmetries are studied. For example, *subtle* directional asymmetries in insect wings have been repeatedly demonstrated, but may be of little adaptive significance, due to limited functional consequences (Klingenberg et al., 1998; Pélabon & Hansen, 2008; Pither & Taylor, 2000). On the other hand, *conspicuous* directional asymmetry in the Cetacean skull has been argued to be related to feeding or biosonar function (Churchill et al., 2019; del Castillo et al., 2016; Huggenberger et al., 2017; Lanzetti, 2022; Macleod et al., 2007); conspicuous directional asymmetry in the skulls of flatfishes relates to their benthic ecology (Evans et al., 2021); conspicuous antisymmetry in many Crustacean appendages has been related to divergent left and right functions (Govind, 1989; Govind & Blundon, 1985; Levinton, 2016; Pratt & Mclain, 2002); and in humans and mice, the mirroring of internal organs, or *situs inversus*, is mostly problematic when only some of the organs are concerned, while complete *situs inversus* entails few health defects (Palmer, 2004).

If one considers that there is not just one left-right (or right-left) body axis, but instead two opposite medio-lateral axes (Meinhardt, 2001; Palmer, 2004), the emergence of conspicuously different left and right phenotypes can be interpreted as the relatively independent expression of two different developmental programs, which can be initiated genetically (e.g. usual *situs solitus*), randomly (e.g. *situs inversus* in *iv* mutant mice, (Brown & Wolpert, 1990)), or environmentally (e.g. lobster claws (Govind, 1989)). It should however be kept in mind that even in extreme cases of antisymmetry (e.g. in fiddler crabs), the development of both sides has been shown to be positively related, at least in terms of resource investment (Levinton, 2016). With this view in mind, in cases of conspicuous directional asymmetry or antisymmetry both medio-lateral axes may be akin to *quasi-autonomous components* (Wagner et al., 2007; Zelditch & Goswami, 2021), producing a special case of modularity in which left and right sides represent developmental modules. In addition to being developmentally modular, each side may also represent a quasi-autonomous functional module, perhaps most obviously in male fiddler crabs which use their minor claw to feed and their major claw for fights and displays, certainly leading to very different selective pressures on the opposite sides of the animal (Pratt & Mclain, 2002). Although the modularity of crab claws has to our knowledge not directly been assessed, studies on the Cetacean skull do suggest a link between directional asymmetry and a modification of the modularity pattern of the skull (Churchill et al., 2019; del Castillo et al., 2016, 2017). The situation in this latter case is slightly more entangled than in the crab claws example, because both sides of the skull, which may develop differently, may be involved in the same function, here feeding or sound production. On the other hand, the general shape of the skull should achieve some degree of symmetry to retain hydrodynamic properties, which would require that some skull modules develop symmetrically, while others develop asymmetrically.

Another case of conspicuous asymmetry, are the mandibles of many insects, among which many Orthopterans, i.e. grasshoppers, crickets and relatives (Ball, 1992; Chapman, 1964; Clissold, 2007). Mandibles are generally used to shear and crush plant material, and their asymmetric shapes allow the distal parts (incisor) to cross and act as double blades, and the proximal parts (molar) to occlude (Clissold, 2007). The left and right mandibles each rotate around an axis formed by two articulation points with the head. They can move independently from each other and, in Orthopterans, are each actuated by one adductor and one abductor muscle which are attached to the inside of the head capsule cuticle (Clissold, 2007). Contrary to the bones of the Cetacean skull, the Orthopteran mandibles remain to some extant physically independent from each other, while contrary to the fiddler crab claws, both mandibles must work together to achieve their feeding function. The Orthopteran head therefore constitutes a somehow intermediate study case of an integrated structure, or *tagma* (Minelli et al., 2013), combining symmetric and asymmetric components, with the left and right asymmetric components being to some extent physically independent, but sharing a common function. In addition to a common function, left and right mandibles share a common developmental origin, being derived from a single of the highly modified head segments (Posnien & Bucher, 2010).

We propose that (i) to achieve conspicuous asymmetry, by which we mean visibly different morphologies on the right and left sides of an animal, the opposite medio-lateral axes of development must have some degree of autonomy from each other, possibly forming modules. At the same time, because overall body (or tagma) symmetry should be generally maintained, we may expect that (ii) asymmetric structures should be to some degree autonomous from symmetric ones, possibly *requiring* some pre-existing level of modularity to allow for asymmetry to arise evolutionarily. (iii) In the case where the left and right asymmetric components must work together to achieve a given function (like the Orthopterans mandibles) and/or when they are physically tightly linked (as in the Cetacean skull), the functional or architectural constraints may also counteract the potential right-left developmental modularity suggested in point (i). Another possibility is that (iv) asymmetries may “spill-over” from conspicuously asymmetrical modules to neighboring areas, for example through asymmetric mechanical loads producing plastic development or reinforcement preferentially on one side or through correlated growth (Levinton, 2016; Pratt & Mclain, 2002; Tiwari et al., 2017).

To test these hypotheses, we focus here on the Orthopteran head morphology, which we quantify using geometric morphometrics. We measure morphological variation in adults at the population level, and decompose it into various types of asymmetries. Taking advantage of the multivariate nature of geometric morphometric data, we study covariation patterns between traits to test different variational modular partitions (Klingenberg et al., 2001; Wagner et al., 2007; Zelditch & Goswami, 2021) and compare them to each other. We expect that mandibles should show strong directional asymmetry, as shown qualitatively in the literature, and that their asymmetrical mechanical actions may induce asymmetry in the neighboring regions, but less so in more distant regions of the head, especially in sensory structures for which symmetry may be functionally advantageous (e.g. compound eyes). Second, we expect that, according to point (i) in the previous paragraph, the left and right mandible may constitute separate modules, allowing their divergent morphologies to emerge, and that they are also quasi-autonomous with regard to the head capsule structures, in which symmetry should be maintained (point (ii)). Alternatively, because the mandibles should enable proper shearing and occlusion, it may be expected as suggested by point (iii), that they are tightly integrated, forming one functional and variational module. If this is the case, it may also be expected that the level of asymmetry is tightly controlled, showing strong adaptive accuracy (Hansen et al., 2006; Pélabon & Hansen, 2008), with individuals deviating from the optimal level of asymmetry having worse biting performance.

Test modularity between left and right halves of the head capsule ignoring mandibles, expect higher correlation than between mandibles